

Middle Eocene Primate Tarsals From China: Implications for Haplorhine Evolution

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ABSTRACT We describe tarsal remains of primates recovered from the Middle Eocene (~45 mya) Shanghuang fissures in southern Jiangsu Province, China. These tarsals document the existence of four higher-level taxa of haplorhine primates and at least two adapid species. The meager and poorly preserved adapid material exhibits some similarities to European adapines like *Adapis*. The haplorhine primates are divided into two major groups: a “prosimian group” consisting of Tarsiidae and an unnamed group that is anatomically similar to Omomyidae; and an “anthropoid group” consisting of Eosimiidae and an unnamed group of

protoanthropoids. The anthropoid tarsals are morphologically transitional between omomyids (or primitive haplorhines) and extant telanthropoids, providing the first postcranial evidence for primates which bridge the prosimian-anthropoid gap. All of the haplorhines are extremely small (most are between 50–100 g), and the deposits contain the smallest euprimates ever documented. The uniqueness of this fauna is further highlighted by the fact that no modern primate community contains as many tiny primates as does the fauna from Shanghuang. *Am J Phys Anthropol* 116: 83–107, 2001. © 2001 Wiley-Liss, Inc.

Over the course of the past several decades, no issue in the study of primate phylogeny has been more contentious than the origin of Anthropoidea, the large clade that today includes New and Old World monkeys, apes, and humans. Various “prosimian” taxa, including adapiforms, omomyids, tarsiids, and tarsiiforms, have been cited as potential stem groups or sister taxa for anthropoids by different workers (e.g., Szalay, 1975; Gingerich and Schoeninger, 1977; Cartmill and Kay, 1978; Szalay and Delson, 1979; Cartmill, 1980; Gingerich, 1980; Rosenberger and Szalay, 1980; Rasmussen and Simons, 1988; Beard et al., 1991; Beard and MacPhee, 1994; Ross, 1994; Simons, 1995). Proponents of each of these different phylogenetic reconstructions have been frustrated by the wide morphological chasm between Anthropoidea and the stem groups or sister taxa they prefer. This problem has been particularly acute for students of postcranial anatomy, leading to disagreements over such fundamental issues as the polarity of numerous postcranial character states among primates as a whole (Ford, 1988, 1994; Dagosto, 1990; Godinot, 1991; Dagosto and Gebo, 1994).

The most direct method of addressing the morphological chasm separating anthropoids from other primates is to recover fossils of basal anthropoid taxa that help to bridge this gap. Fossils of such basal taxa can be crucial to phylogeny reconstruction because they often possess unique combinations

of characters that can illuminate the origins of the higher taxa to which they pertain (e.g., Gauthier et al., 1988). On the other hand, the phylogenetic affinities of allegedly basal members of higher-level taxa are almost inherently controversial, and for the same reasons that these taxa are potentially pivotal to phylogeny reconstruction. Their unique combinations of primitive and derived characters can yield highly unstable phylogenetic tree topologies, especially when the fossil taxa in question are documented only by incomplete anatomical material.

Given this context, it is not surprising that the discovery of the extinct primate family Eosimiidae has both advanced and intensified the ongoing debate over anthropoid origins. If eosimiids are basal anthropoids, as those who have been involved in their discovery and initial description unanimously agree (Beard et al., 1994, 1996; MacPhee et al., 1995; Jaeger et al., 1999; Gebo et al., 2000a,b), then not only do these animals clarify the phylogenetic position of anthropoids with respect to other primates,

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but they also provide new data concerning the chronology and paleobiogeography of anthropoid origins. Hypotheses regarding functional and paleoecological aspects of anthropoid origins are similarly constrained.

However, the anthropoid affinities of eosimiids have been disputed (Godinot and Mahboubi, 1994; Godinot, 1994; Simons and Rasmussen, 1994; Simons, 1995; Rasmussen et al., 1998). Without doubt, part of the basis for this lack of consensus about the anthropoid affinities of eosimiids derives from the incomplete anatomical information published for this group to date. With two recent exceptions (Gebo et al., 2000a,b), previously published descriptions of eosimiid anatomy have been confined to the jaws, the upper and lower dentition, and a single petrosal bone.

Of the sites that have yielded eosimiids so far, the most abundantly fossiliferous are fissure-fillings near Shanghuang village, in Liyang County, southern Jiangsu Province, People's Republic of China. These fissures preserve diverse fossil vertebrate assemblages that include adapiform, omomyid, tarsiid, and eosimiid primates (Beard et al., 1994; MacPhee et al., 1995), brontotheriid perissodactyls (Qi and Beard, 1996), cricetid rodents (Wang and Dawson, 1992), and many other taxa (Qi et al., 1996). Biostratigraphic evidence from the fossil mammalian faunas indicates that the Shanghuang fissure-fillings date to the Middle Eocene, roughly 45 mya.

Here, we describe numerous primate tarsal bones from the Shanghuang fissure-fillings. These tarsals document a taxonomically diverse primate assemblage, as is to be expected on the basis of an earlier study of primate dental remains from these fissures (Beard et al., 1994). Given the high diversity of primates and the absence of articulated skeletal remains at the Shanghuang fissure-fillings, it is not always clear how postcranial elements correspond to formally designated species, which are conventionally erected on the basis of jaws and dentitions. What is clear is that many of the tarsals described here pertain to taxa that have not yet been named. As a result, we have simply segregated the Shanghuang tarsals into broad morphological categories that permit them to be described and interpreted prior to the publication of a synthetic analysis of the systematics of the Shanghuang primates.

In this paper we use the family Omomyidae to include taxa usually referred to the Anaptomorphinae and Omomyinae, but microchoerine primates are placed in a separate family, the Microchoeridae (Schmid, 1981). Tarsiiformes include the Omomyidae, Microchoeridae, and Tarsiidae. Following Szalay and Delson (1979), we include both Adapiformes and Lemuriformes in the suborder Strepsirhini, and Tarsiiformes and Anthropoidea in the suborder Haplorhini. Following MacPhee et al. (1995), we use the informal term "telanthropoids" for the higher level group that

includes Oligopithecidae, Parapithecidae, Platyrrhini, and Catarrhini.

MATERIALS AND METHODS

Currently, 50 tarsal specimens have been identified from Shanghuang fissures A, C, D, and E. The fissures are roughly contemporaneous, with fissures D and E being slightly older (Wang and Dawson, 1992; Beard et al., 1994). Each fissure spans a 1–2 million year interval (Beard et al., 1994). All of the tarsals have been recovered from screening and represent isolated remains with no dental associations. Many of the specimens are broken, and they often display chemically etched surfaces suggesting bird predation (Andrews, 1990). A large component of the Shanghuang mammalian fauna may represent the remains of ancient owl pellets. As a consequence, the fauna may be biased for small size; many other Shanghuang mammals (mostly rodents, lagomorphs, and insectivores) are also of small size, and the remains of small lizards and amphibians are also common.

Tarsal morphological features and measurements are after Gebo (1988) and Gebo et al. (1991) (Figs. 1, 2). The tarsal bones were measured with microscope and reticle. The morphological comparisons are made from the following groups and samples: Adapiidae (8 taxa and 88 tarsals), Omomyidae (9 taxa and 64 tarsals), Tarsiidae (2 taxa and 30 tarsals), Cebinae (11 taxa and 72 tarsals), Callitrichinae (7 taxa and 119 tarsals), Parapithecidae (2 taxa and 9 tarsals), and Propithecidae (2 taxa and 4 tarsals).

All specimens are permanently accessioned in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, China, and each specimen is catalogued separately, using the IVPP's V designation and a number (V = vertebrate fossil).

RESULTS

Shanghuang haplorhines

Allocation and body size. On the basis of tarsal morphology, four groups of haplorhine primates are recognized at Shanghuang, including two new forms as yet unnamed (Figs. 3, 4). Two groups are prosimian-like and two are anthropoid-like. The prosimian group contains two very similar morphs: a group which is virtually indistinguishable from North American omomyids (morphology 1), and tarsiids (morphology 2). True omomyids are known in Asia (Beard and Wang, 1991), but since there are as yet no omomyid dental remains at Shanghuang, save for *Macrotarsius*, we have allocated morphology 1 tarsals to an unnamed group called "unnamed haplorhine family." All of these tarsals are too small to be allocated to *Macrotarsius*, a 1-kg primate. The anthropoid-like group also contains two taxa: Eosimiidae (morphology 3), and a morphologically different group we call "new protoanthropoids" (morphology 4).

Within each morphological group there are a variety of sizes (Table 1). Size classes within each

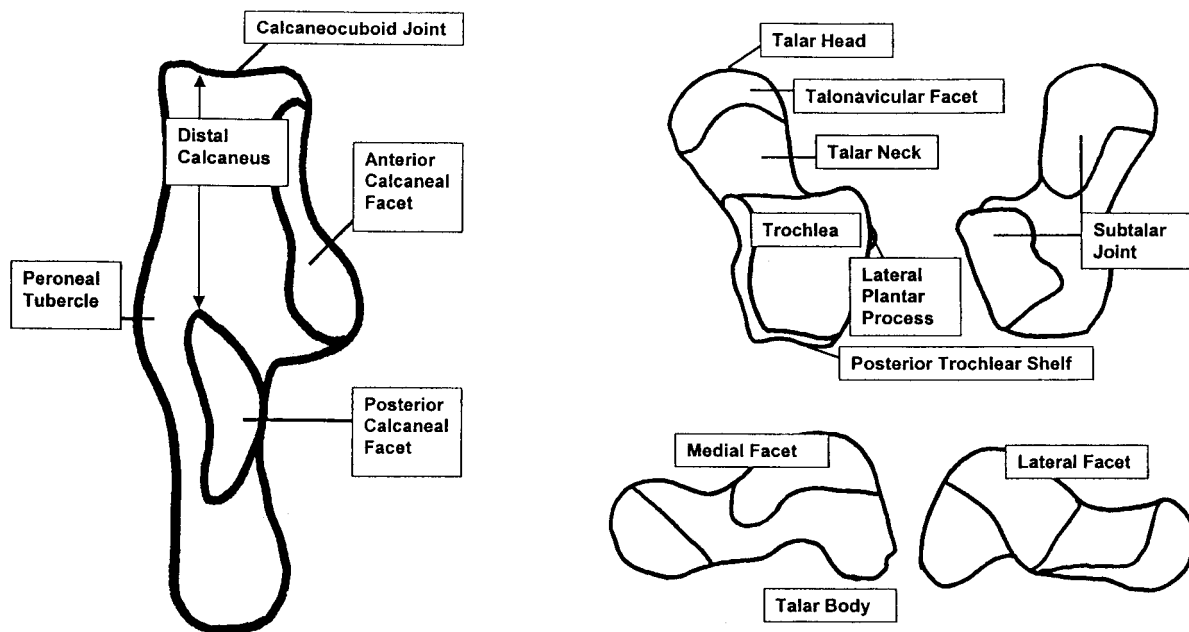


Fig. 1. Tali and calcanei features.

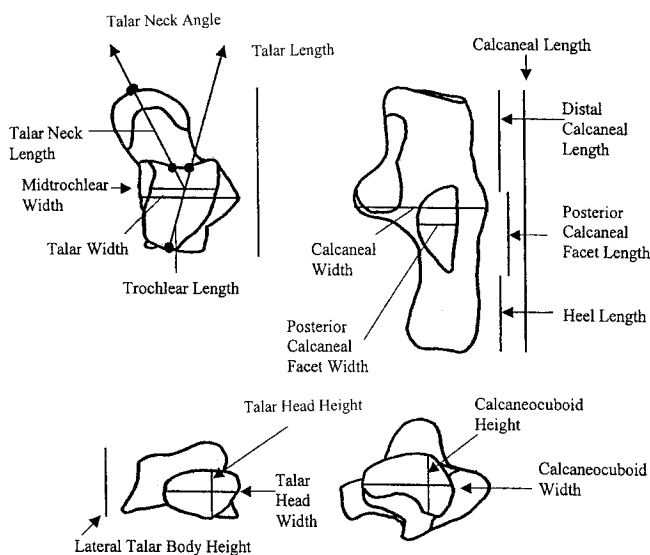


Fig. 2. Tali and calcanei measurements.

group were assessed by several methods: by eye, by predicting size based on strepsirhine regression equations in Dagosto and Terranova (1992), and by position on the first axis of a principal component analysis (Payseur et al., 1999). Based on morphology and size, 12–16 species-level taxa are represented within this sample. Most of these taxa are between 50–100 g (Table 1), but taxa as small as 10–20 g are also present.

Calcanei. Thirty calcanei from four Shanghuang fissures (A, C, D, and E) have been identified as pertaining to haplorhine primates. It is more difficult to distinguish the calcanei of strepsirhine and haplorhine primates than is the case for other tarsal elements, particularly the talus (Beard et al., 1988).

The majority of Shanghuang specimens, however, are too small to belong to the adapiforms currently recognized from this site. Moreover, all of the tali that have been recovered from Shanghuang in the same size range as these calcanei clearly represent haplorhine primates. The posterior calcaneal facet is generally longer and narrower (index $pcfw/pcf$, Table 2) in adapiforms (but not extant lemurs) than is the case in extant or fossil haplorhines. In adapiforms, the posterior calcaneal facet is well-delimited along its plantar edge, while in haplorhines the plantar edge of the posterior calcaneal facet blends into the calcaneal surface. In omomyids and anthropoids (but not *Tarsius*) there is a gap between the anterior calcaneal tubercle and the articular surface of the calcaneocuboid joint. In contrast, the anterior calcaneal tubercle contacts the joint surface in adapiforms (but not in extant lemuriforms). Because the Shanghuang specimens exhibit the characteristics of haplorhine calcanei, rather than adapiform, they are assigned to the former group here.

Morphology 1. Prosimians: unnamed haplorhine family (fissures A, D, E; specimens V 11847, V 11853, V 12275, and V 12276; Table 3)

Allocation. Four Shanghuang calcanei represent basal haplorhine primates and are designated as morphology 1 (Fig. 5). Two of these calcanei are from fissure A (V 11847 and V 12276), while the others come from fissures D (V 12275) and E (V 11853). The two calcanei from fissures D and E are similar in size and morphology, and may therefore belong to the same genus and species. In contrast, the two calcanei from fissure A differ dramatically from each other in size and in some aspects of morphology. Thus they likely represent two distinct genera. As of yet, none of these calcanei have been matched with



Fig. 3. Dorsal view of four types of haplorhine calcanei (Shanghuang, China). Left to right: IVPP V 12288, V 11851, V 11856, and V 11853. Scale bar = 2 mm.

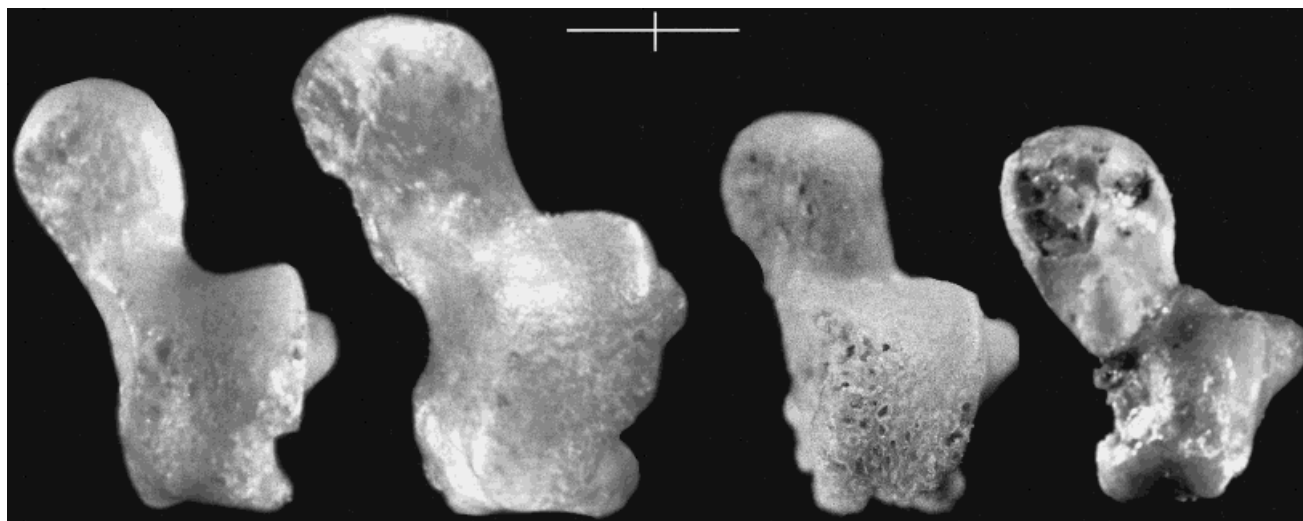


Fig. 4. Dorsal view of four types of haplorhine tali (Shanghuang, China). Left to right: IVPP V 12306, V 11855, V 11854, and V 11857. Scale bar = 2 mm.

dental specimens on the basis of size and locality. Thus, no names have been given to these taxa.

On the basis of morphology, these four calcanei are most similar to those of North American omomyids. One omomyid, *Macrotarsius*, is in fact known from fissure D (where it is very rare). The large size of *Macrotarsius macrorhysis* (900–1,221 g; MacPhee et al., 1995) prevents it from being associated with any of these calcanei, which represent much smaller primates. We are left with two possibilities. Either dental remains of several tiny omomyids remain to be found at fissures A, D, and E; or these four cal-

canei belong to a new (probably family-level) taxon of haplorhine primates. The latter option seems more likely to us at this stage. However, the systematic affinities of undescribed haplorhine dentitions from the Shanghuang fissures require further study before any definitive choice between these possibilities can be reached.

Size. There are three size classes within this group. V 12275 and V 11853 are similar in size (Table 3), both yielding mass estimates of 20–30 g (Table 1), which is similar to that of the smallest

TABLE 1. Body size estimates for calcanei and tali (in grams)¹

Specimens	Fissure	Calcaneal width	Cuboid width	Cuboid width × cuboid height	pcf length	pcf width	Mean	Size class		
Unnamed haplorhines										
Calcanei	V 11847	A	15.4	12.2	9.8	16.4	8.2	12.4	1	
	V 11853	E	39.2	39.7	34.6	12.8	19.2	29.1	2	
	V 12275	D	50.5	35.1	30.9	24.5	41.9	36.6	2	
	V 12276	A	204.2			500.7	354.2	353.0	4	
Tali										
Tali	V 11857	D	45.1	68.8				56.9	2/3	
	V 12297	A	28.8		41.0			34.8	2	
	V 12298	D	68.5	128.2	95.1			97.3	3	
	V 12299	D	53.5	117.7	79.9			83.7	3	
	V 12300	D			40.3			40.3	2	
Tarsiidae										
Calcanei	V 11856	D	33.2			28.1	20.5	27.3	1	
	V 12277	D	23.6			19.4	25.3	22.7	1	
	V 12278	D	25.5			27.1	37.8	30.1	1	
	V 12279	D				83.4	74.8	79.1	2	
	V 12310	D				40.6	10.3	25.5	1	
	V 12311	D				123.5	57.0	90.3	2	
	V 11854	D	59.0	62.9	96.5			72.8	2	
Eosimiidae										
Calcanei	V 11848	D	23.6	22.2	15.9	18.5	6.4	17.3	1	
	V 11851	C	96.8	66.0	40.2	56.2	37.2	59.3	3	
	V 12280	A	127.6	96.2	68.4	109.9	45.7	89.6	4	
	V 12281	A	127.6	81.3	56.5	91.4	52.6	81.9	4	
	V 12282	A	71.2			85.7		78.5	4	
	V 12283	A				138.1	57.0	97.6	4	
	V 12284	D	92.1	68.9	43.7	120.7	49.7	75.0	3	
	V 12285	D	39.7	22.2	18.5	40.7	19.0	28.0	2	
	V 12286	E	157.8	122.3	81.5	138.1	57.0	111.3	5	
	V 12313	D	171.8	129.3	109.3	138.1	49.5	119.6	5	
	V 12314	D	185.8			138.1	37.1	120.3	5	
	V 12315	D	27.6			20.7	6.4	18.2	1	
	Tali	V 11849	D	65.5	119.4	121.4			102.1	5
		V 11855	D	97.4	134.2	121.4			117.7	5
V 12301		D	59.5		59.3			59.4	3	
V 12302		D	54.5		121.4			87.9	4	
V 12303		D	70.4	105.7	113.6			96.6	4	
V 12304		E	50.5	50.7	68.6			56.6	3	
V 12312		D	71.2		79.5			75.4	4	
New protoanthropoids										
Calcanei	V 12287	A	47.5			20.7	15.7	28.0	1	
	V 12288	D	157.8			85.7	73.7	105.7	4	
	V 12289	D	83.3			60.5	22.8	55.6	2	
	V 12290	D	127.6			75.0	43.1	81.9	3	
	V 12291	D	150.2			123.5	73.7	115.8	4	
	V 12292	D	94.9			56.2	37.2	62.8	3	
	V 12293	D				138.1	63.3	100.7	3/4	
	V 12294	D	95.8	55.2		109.9	37.2	65.6	3	
	V 12295	E	92.1	55.2		48.0	19.0	49.7	2/3	
	V 12296	E	192.2			103.5	73.7	123.1	5	
	Tali	V 12305	C	64.2	76.2	53.6			64.7	3
		V 12306	C	53.0	70.8	84.5			69.4	3

¹ pcf, posterior calcaneal facet; mtrw, midtrochlear width.

living primate, *Microcebus myoxinus* (30.6 g; Atsalis et al., 1996). In terms of their absolute length, the V 12275 and V 11853 calcanei are similar to those of *Teilhardina belgica*, which is one of the smallest known omomyids. These Shanghuang calcanei are much smaller than those of other omomyids, including *Shoshonius*, *Washakius*, *Absarokius*, and UCM 58658 (Covert and Williams, 1994). V 12276 is by far the largest specimen in this group (its body mass is estimated at over 300 g). In contrast, V 11847 is the tiniest of the four calcanei in this group (its body

mass is estimated at only 12 g). The unnamed species represented by this calcaneus may well be the smallest primate ever documented (Gebo et al., 2000a).

Morphology. These calcanei have distal segments that comprise 53–60% of the total length of the calcaneus (distal length/calcaneal length; Table 3). All except V 11847 (53%) have calcanei that are more distally elongated than is typical in omomyids. As a result of this increased calcaneal length, these

TABLE 2. *Calcanei ratios*¹

	No.	CalW/CalL	DistL/CalL	PcfL/CalL	HeelL/CalL	PcfL/HeelL	PcfW/PcfL	CubW/CubHt
Omomyids								
<i>Teilhardina belgica</i>	5	36 (35–36)	51 (47–54)	23 (20–26)	26 (26–27)	88 (79–100)	64 (50–75)	
<i>Tetonius</i> (composite)	2	*34	*49	*23	*28	82	59	138
<i>Absarokius abbotti</i>	1	37	56	22	22	101	54	112
<i>Shoshonius cooperi</i>	2	33 (30–36)	53	23	23	101	56	150
? <i>Omomys</i>	3, 14	31	53 (50–55)	19 (18–20)	26 (26–27)	71 (60–84)	67 (54–79)	125 (120–130)
? <i>Hemiacodon gracilis</i>	4, 9	32 (30–32)	52 (50–54)	20 (18–21)	29 (27–30)	68 (60–78)	69 (62–79)	134 (128–150)
<i>Washakius insignis</i>	2	32	52	26	24	108	55	118
<i>Arapahovius gazini</i>	1	34	54	25	21	121	61	
<i>Necrolemur zitteli</i>	1	*19	*65	*19	*16	119	71	
<i>Microchoerus edwardsi</i>	1	*33	*50	*35	*15	233	58	
Tarsiids								
<i>Tarsius syrichta</i>	9	13 (13–14)	77 (76–77)	12 (10–13)	12 (11–14)	103 (81–112)	54 (46–63)	105 (82–125)
<i>Tarsius bancanus</i>	6	14 (11–14)	76 (76–77)	12 (12–13)	13 (11–14)	97 (85–114)	55 (47–60)	103 (82–122)
Platyrrhines								
<i>Cebupithecia sarmientoi</i>	1	55	42	36	22	167	59	153
<i>Cebuella pygmaeus</i>	7	52 (45–54)	41 (36–44)	37 (33–41)	22 (15–30)	161 (110–189)	62 (51–67)	134 (113–152)
<i>Callithrix jacchus</i>	10	53 (50–56)	41 (36–43)	31 (28–37)	28 (27–34)	116 (82–152)	71 (62–77)	114 (110–134)
<i>Callithrix argentata</i>	6	52 (51–53)	42 (39–46)	33 (31–34)	27 (20–32)	127 (100–168)	70 (64–83)	123 (109–140)
<i>Saguinus leucopus</i>	2	54 (54)	44 (42–45)	34 (33–34)	23 (22–23)	149 (148–150)	72 (67–78)	143 (137–148)
<i>Saguinus midas</i>	4	52 (50–53)	40 (36–44)	36 (34–37)	24 (19–30)	155 (113–194)	66 (63–69)	130 (116–147)
<i>Saguinus oedipus</i>	20	51 (46–59)	40 (36–43)	34 (30–38)	27 (20–30)	130 (103–193)	70 (56–81)	125 (112–153)
<i>Callimico goeldi</i>	10	52 (49–54)	41 (37–44)	36 (35–39)	23 (18–27)	162 (130–216)	70 (66–75)	119 (111–130)
<i>Saimiri sciureus</i>	9	52 (48–56)	46 (43–49)	33 (30–36)	21 (19–24)	158 (129–181)	61 (46–68)	130 (120–151)
<i>Cebus apella</i>	6	50 (46–53)	42 (39–44)	28 (25–31)	30 (28–33)	95 (76–111)	81 (75–93)	131 (122–148)
<i>Cebus capucinus</i>	6	56 (50–63)	41 (39–43)	31 (28–33)	28 (26–34)	112 (83–125)	70 (68–73)	136 (129–145)
<i>Cebus albifrons</i>	2	53 (48–59)	43 (42–43)	31 (28–34)	26 (23–30)	122 (93–150)	73 (70–75)	123 (119–127)
<i>Callicebus torquatus</i>	2	54 (53–55)	40 (38–42)	37 (36–38)	23 (22–24)	160 (159–161)	62 (53–71)	138 (136–140)
<i>Callicebus donaphilus</i>	3	56 (55–56)	42 (40–45)	34 (31–36)	24 (23–24)	143 (130–151)	73 (70–79)	135 (120–143)
<i>Aotus trivirgatus</i>	7	49 (46–52)	44 (41–47)	31 (30–34)	25 (20–29)	129 (107–166)	70 (60–77)	134 (120–142)
Adapiforms								
<i>Cantius mckennai</i>	3, 5	44 (43–47)	44 (43–45)	29 (27–30)	28 (25–30)	104 (89–120)	52 (47–53)	124
<i>Cantius trigonodus</i>	5	41 (38–44)	41 (37–45)	32 (29–35)	27 (24–33)	113 (88–149)	45 (42–51)	124 (117–132)
<i>Cantius abditus</i>	3, 8	43 (40–46)	41 (37–44)	32 (30–34)	27 (24–33)	117 (104–134)	49 (45–53)	135 (127–147)
<i>Notharctus tenebrosus</i>	2, 3	42 (40–45)	36 (35–36)	34 (32–35)	30 (29–32)	111 (101–121)	52 (51–54)	116
<i>Notharctus pugnax</i>	2, 6	44 (43–45)	40 (31–45)	32 (29–38)	28 (23–31)	116 (95–139)	51 (42–60)	145 (132–158)
<i>Smilodectes gracilis</i>	1, 5	42 (37–47)	38 (37–39)	31 (30–32)	31 (31–32)	98 (92–104)	50 (49–51)	147 (140–153)
<i>Adapis parisiensis</i>	3, 5	38 (31–42)	32 (28–41)	32 (19–38)	36 (24–44)	89 (75–113)	60 (40–67)	174 (143–204)
<i>Leptadapis magnus</i>	3	36 (31–41)	31 (25–38)	32 (26–37)	36 (30–42)	93 (63–111)	52 (45–58)	138 (119–172)
<i>Europolemur</i> (Messel)	1		37	34	29	117		

¹ CalW, calcaneal width; CalL, total calcaneal length; DistL, distal calcaneal length; PcfL, length of posterior calcaneal facet; HeelL, length of heel; CubW, calcaneocuboid facet width; CubHt, calcaneocuboid facet height; *, estimated values; (), range of values.

specimens are narrow relative to their widths (calcaneal width/calcaneal length, 27–39%; Table 3). Despite the lengthening of these bones, the heel (12–25% of total length) and the posterior calcaneal facet (pcf; 15–29%) remain relatively long. V 12275 and V 11853 have longer heels and shorter posterior calcaneal facets than the calcanei from fissure A.

The posterior calcaneal facet is wide relative to its length (pcfW/pcfL) in V 12275 and V 11853, but the new haplorhine calcanei from fissure A have longer, narrower facets like those of omomyids. The distal edge of the posterior calcaneal facet relative to the posterior or proximal edge of the sustentaculum tali is located in the same plane of orientation in V 11847, V 11853, and V 12275, as is the case in *Shoshonius* and *Tetonius*. In contrast, V 12276 and *Washakius* show a posterior shift in the position of this facet relative to the edge of the sustentaculum tali, which is located at a more midfacet position in these latter forms.

As is typical of most primates, V 11847, V 12275, and V 11853 each have a continuous anterior calca-

neal facet (Gebo, 1989). V 12276 exhibits a separated distal facet. This type of facet arrangement has been noted to occur in calcanei attributed to East African Miocene “lorisids” (KNM-SO-1364 and 1365; Gebo, 1986b) as well as in cercopithecids (Strasser and Delson, 1986; Szalay and Langdon, 1986; Strasser, 1988) and parapithecids (Gebo, 1989). This arrangement of distal calcaneal facets has never been documented in omomyids.

All four of the new haplorhine calcanei share a similar morphology of the calcaneocuboid joint. This region is wide and very flat, with a shallow pivot situated at the lower center of the joint surface. These conditions are most reminiscent of omomyids like *Washakius*, *Tetonius*, and *Shoshonius*. *Hemiacodon* and ?*Omomys*, in contrast, possess much deeper depressions around the pivot region. All four of these Shanghuang calcanei possess a prominent anterior calcaneal tubercle for the short and long plantar ligaments (ligaments which maintain the association between the calcaneus and cuboid).

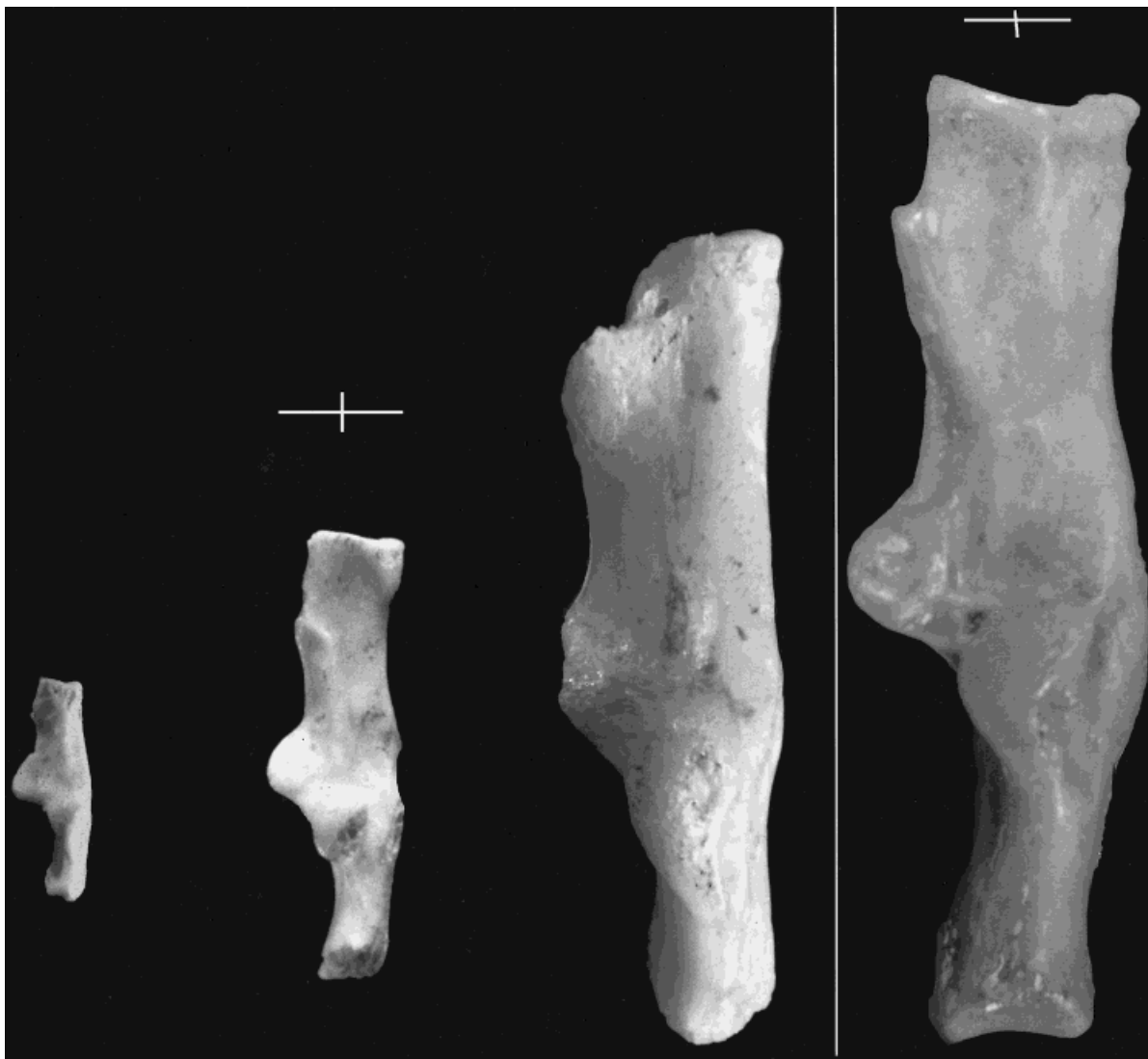


Fig. 5. Left: Dorsal view of three “unnamed haplorhine” right calcanei. Left to right: IVPP V 11847, V 11853 and V 12276. Right: *Hemicacodon*. Scale bar = 2 mm.

All four of these new haplorhine calcanei from Shanghuang have very small peroneal tubercles. However, V 12275 and V 11853 possess wider peroneal tubercles than do either of the calcanei from fissure A. V 12275 possesses an indentation in this region rather than the single arc that occurs here in most other primates, and the peroneal tubercle is more distal in its origin. V 12276 is extremely narrow at this transverse section of the calcaneus.

Within-group comparisons. The calcanei included in this group show a general similarity to those of omomyids. However, different morphs are apparent among these new haplorhines. V 12275 and V 11853 closely resemble each other, although these specimens were recovered from different fissures. Both of these specimens differ from V 11847 and V 12276, the calcanei from fissure A. V 12275 and V 11853 each possess very long distal segments (57% and 60% of total calcaneal length, respective-

ly), being longer than most omomyids but similar to *Microcebus* in this regard (Table 3). As a result, they also have relatively shorter posterior calcaneal facets than do omomyids or the other unnamed haplorhine calcanei from Shanghuang. On the other hand, like omomyids, they have relatively long heels compared to the other unnamed haplorhines. V 12275 and V 11853 have short and relatively wide posterior calcaneal facets compared to the calcanei from fissure A. V 12275 and V 11853 share similar calcaneal width-to-length ratios and distal elongation ratios with the much larger calcaneus from fissure A (V 12276, Table 3), while V 11847 differs from all the other calcanei in these respects. The lateral calcaneal edge dips inward in V 12275 and V 11853, in contrast to the more or less straight edge in V 12276. The lateral calcaneal edge of V 11847 is gently curved. The lateral distal calcaneal region is pinched more distally in V 11847, V 11853, and V

TABLE 3. Measurements (in mm) and ratios for unnamed haplorhine calcanei¹

	V 11847	V 11853	V 12275	V 12276	<i>Microcebus</i> (n = 10)	<i>Shoshonius</i> (n = 2)
Calcaneal length (cl)	4.00	6.95	7.37	14.07	10.02	9.79
Distal length (dl)	2.10	4.15	4.17	8.33	6.10	5.20
pcf length (pcf)	1.15	1.05	1.33	4.00	2.06	2.23
pcf width (pcfw)	0.70	0.90	1.14	2.16	1.68	1.25
Heel length (hl)	0.75	1.75	1.87	1.74	1.86	2.22
Width of cal-cuboid facet (ccw)	1.00	1.55	1.48		1.78	2.32
Height of cal-cuboid facet (cch)	0.80	1.25	1.21	2.34	1.12	1.55
Calcaneal width (cw)	1.55	2.15	2.35	3.83	2.58	3.25
dl/cl	0.53	0.60	0.57	0.59	0.61	0.53
cw/cl	0.39	0.31	0.32	0.27	0.26	0.33
hl/cl	0.19	0.25	0.25	0.12	0.19	0.23
pcf/cl	0.29	0.15	0.18	0.28	0.21	0.23
pcf/hl	1.53	0.60	0.71	2.30	1.11	1.01
pcfw/pcf	0.61	0.86	0.86	0.54	0.82	0.56
ccw/cch	1.25	1.24	1.22		1.59	1.50

¹ The extant lemur *Microcebus* and the omomyid *Shoshonius* are included for comparison. cal, calcaneal; pcf, posterior calcaneal facet.

12276, as it is in *Teilhardina*. This pinching occurs more proximally in V 12275, as is the case in *Hemiacodon*, *?Omomys*, *Shoshonius*, and *Washakius*.

V 11847 also differs from the other new haplorhines in other aspects of calcaneal shape. The anterior calcaneal facet of this specimen is very cupped at the midfacet region, whereas the other unnamed haplorhine calcanei possess flatter, less-curved anterior facets. This midfacet cupping changes the anterior and posterior angles of this facet relative to the condition in the other calcanei, and it holds the talar neck and head more securely during inversion and eversion movements of the foot.

V 11853 and V 12275 differ from the similar-sized calcanei of *Teilhardina* in being distally longer, in possessing shorter and wider posterior calcaneal facets, and in being slightly narrower. The V 11847 calcaneus is relatively wider than those of omomyids and the other unnamed haplorhine calcanei from Shanghuang (see calcaneal width/length, Table 3).

Summary. All of these “unnamed haplorhine” calcanei belong to very tiny primates and all possess moderately long distal regions. These calcanei are extremely similar in form to those attributed to omomyids; both possess calcaneal elongation in the moderate range seen in extant cheirogaleids. This degree of tarsal elongation is mechanically associated with quadrupedal-leaping primates and implies locomotor similarities to primates like *Microcebus*. Cheirogaleids are known for their quick and agile movements, including quadrupedalism, climbing, and quadrupedal suspensory movements (Gebo, 1987b). The long subtalar joint in these new haplorhine taxa implies good subtalar, and thus foot, mobility for climbing or grasping. In this group there are two different morphologies of the posterior calcaneal facet. In V 11847 and V 12276, the posterior calcaneal facet is long relative to the heel but short in width relative to facet length. In contrast, V 11853 and V 12275 have a short facet that is less than the length of the heel region. Short facets are generally associated with more leaping-oriented pri-

mates, while longer facets are generally associated with climbing primates like lorises (Gebo, 1988). In this case, however, V 12276 has the second longest distal calcaneus combined with a long posterior calcaneal facet, implying a mixture of traits associated with locomotor function.

Morphology 2. Prosimians: tarsiids (fissure D, specimens V 11856, V 12277–12279, V 12310, and V 12311; Table 4)

Allocation. Six calcanei from fissure D differ in shape from those attributed to the “unnamed family” of haplorhines. These calcanei (Fig. 6), although very similar overall to the “unnamed haplorhine” group (Fig. 3), share a few morphological similarities with extant *Tarsius* and on this basis are best allocated to the Tarsiidae. *Tarsius eocaenus*, the only tarsiid from the Shanghuang fissures described on the basis of dental remains to date, has only been reported from fissures A and C (Beard et al., 1994). However, *Tarsius eocaenus* is appropriate in size, similar to that estimated for V 11856, V 12277, V 12278, and V 12310.

Size. Two size classes are apparent at fissure D, suggesting at least two species-level taxa. V 11856, V 12277, V 12278, and V 12310 represent very small primates (20–30 g), while V 12279 and V 12311 are estimated to be three times as large (80–90 g). With the possible exception of *T. pumilus*, all of the Shanghuang tarsiid calcanei appear to pertain to species much smaller than living *Tarsius* (100–150 g).

Morphology. All six calcanei are broken distally, with V 11856 representing the most complete bone. We cannot therefore calculate the segment/length ratios for these calcanei, except to note that relative distal length would have been greater than 50% in V 11856. The calcanei are very narrow, and all six show a progressive narrowing of the distal calcaneal region reminiscent of *Tarsius*. Neither omomyids nor the new haplorhines show such narrowing.

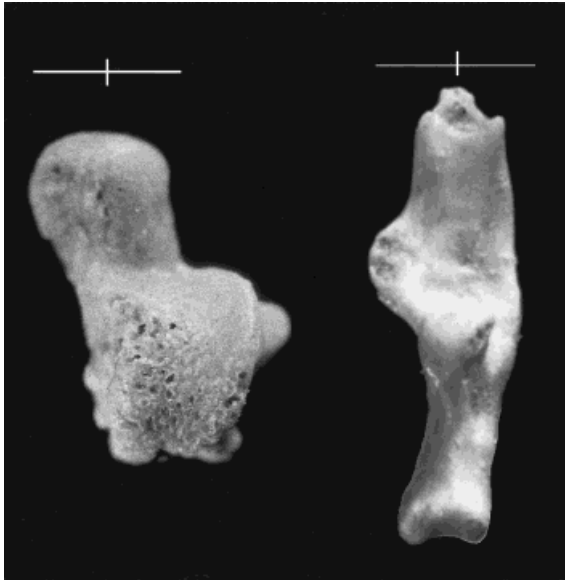


Fig. 6. Dorsal view of a Shanghuang right tarsiid talus (IVPP V 11854) and calcaneus (IVPP V 11856). Scale bar = 2 mm.

The posterior calcaneal facet is short relative to the heel in V 11856, V 12277, V 12278, and V 12311, while V 12279 and V 12310 possess a facet longer than the heel (pcf length/heel length, Table 4). The pcf width/length ratios show V 11856, V 12279, V 12310, and V 12311 to be very similar, while V 12277 and V 12278 have higher values (i.e., a wider facet). All of these values, however, are similar to those calculated for the unnamed haplorhine calcanei, tarsiers, and omomyids. The anterior calcaneal facet is continuous on the best-preserved specimen, V 11856. Like that of *Tarsius*, the peroneal tubercle is very small in all of these calcanei. The calcaneocuboid joint, one of the most diagnostic regions of the calcaneus of *Tarsius*, is unfortunately not preserved in any of these specimens. Given the long and narrow distal calcaneus, we suggest that leaping played a greater functional role in the locomotor behavior of these taxa than was the case in the “unnamed haplorhine” morphological group.

Morphology 3. Protoanthropoids: eosimiids
(fissures A, C, D, and E; specimens V 11848,
V 11851, V 12280–12286, and
V 12313–12315; Table 5)

Allocation. This morphology is the only one to be represented in all four fissures (Fig. 7). Like the other Shanghuang calcanei, none of these specimens is associated with dentitions, making all allocations tentative. The body mass of *Eosimias sinensis* from fissure B as estimated from molar area is 67–137 g (Beard et al., 1994), which fits well with size classes 2–5 (Table 1). Undescribed dental material pertaining to other species of Eosimiidae exist at these fissures in the size range appropriate for these calcanei. *Adapoides* and *Macrotarsius* are also known from fissure D (Beard et al., 1994), but these prosimian taxa are too large to possess calcanei of

this size. There are also morphological reasons which make allocation to Eosimiidae the most likely. As discussed below regarding the talus, the Locality 1 talus from Shanxi Province, China almost certainly belongs to *Eosimias centennicus*. The morphology-3 tali from Shanghuang are morphologically identical to the Locality 1 talus, and are therefore also attributed to eosimiids. Morphology-4 tali must then be attributed to another basal anthropoid group. Morphology-4 tali are distinguished from morphology-3 tali in part by a higher neck angle, which implies a calcaneus with a wider sustentaculum tali. The Shanghuang calcanei bearing a wide sustentaculum tali are therefore attributed to morphology 4. By default, the remaining protoanthropoid calcanei must be assigned to morphology 3, eosimiids.

Size. Among these 12 calcanei there are 3–5 size classes. No specimen is estimated to pertain to a primate weighing more than 130 g (mean weight). Calcaneal length and width values show a similar size distribution. It seems quite probable that at least three species are present in this sample on the basis of calcaneal size.

Morphology. Compared to the prosimian haplorhine groups (Fig. 3), the calcanei assigned to Eosimiidae have relatively shorter distal calcaneal regions (45–52%). Indeed, the two groups do not overlap in this feature. The eosimiid values, though higher than those of many extant telanthropoids, are similar to those of *Saimiri* (Table 2). As a result of being relatively short distally, eosimiid calcanei are also relatively wide, being a little narrower than in most platyrrhines but wider than in omomyids or tarsiids. Despite the calcaneus being shorter, the heel is the same proportion of total calcaneal length in eosimiids (21–26%) as in the unnamed haplorhines or omomyids, meaning that the heel must be absolutely shorter in this taxon. This is also true in platyrrhines (21–30%; Table 2). In contrast, adapids have short distal calcanei like telanthropoids and eosimiids, but retain a long heel (28–36% of total calcaneal length; Table 2).

The pcf length/heel length ratio is generally greater than 100 in eosimiids, as is also typical of platyrrhines. Tarsiers and omomyids generally have lower ratios. On the other hand, eosimiid calcanei have a relatively long and narrow posterior calcaneal facet (pcf width/pcf length ratio, 48–61%), which is more like that of prosimians than the shorter, broader facet of telanthropoids. The anterior calcaneal facet is continuous on all the calcanei assigned to this group. The peroneal tubercles are small.

The calcaneocuboid joint of morphology 3 is intermediate between “prosimians” and telanthropoids (Fig. 8). The primitive condition for primates, exhibited by notharctines and omomyids, is a broad, flat, fan-shaped surface with a centrally located pivot. In contrast, telanthropoids possess a joint surface that resembles a circle with a small wedge removed from

TABLE 4. Shanghuang tarsiid calcaneal measurements (in mm) and ratios¹

	V 11856	V 12277	V 12278	V 12279	V 12310	V 12311	<i>Tarsius syrichta</i> (n = 9)
Calcaneal length (cl)							25.60
Distal length (dl)							19.41
pcf length (pcfl)	1.40	1.22	1.38	2.20	1.60	2.40	3.03
pcf width (pcfw)	0.92	0.98	1.11	1.35	0.75	1.25	1.62
Heel length (hl)	2.00	1.89	2.10	1.90	1.50	2.70	3.16
Cal-cuboid width (ccw)							2.33
Cal-cuboid height (cch)							2.24
Calcaneal width (cw)	2.03	1.80	1.85				3.42
dl/cl							0.77
cw/cl							0.13
hl/cl							0.12
pcfl/cl							0.12
pcfl/hl	0.70	0.65	0.66	1.16	1.06	0.88	1.03
pcfw/pcfl	0.66	0.80	0.80	0.61	0.47	0.52	0.54
ccw/cch							1.05

¹ The extant tarsier, *Tarsius syrichta*, is presented for comparison.

TABLE 5. Calcaneal measurements (in mm) and ratios for the eosimiid calcanei¹

	V 11848	V 11851	V 12280	V 12281	V 12282	V 12283	V 12284	V 12285	V 12286	V 12313	V 12314	V 12315	<i>Cebuella pygmaea</i> (n = 7)
Calcaneal length (cl)	4.25	6.60	7.90	7.50		7.60	7.66		8.20	8.2			7.46
Distal length (dl)	2.20	3.10	3.90	3.50	3.55	3.40	3.48		4.00	3.9	4.0		3.02
pcf length (pcfl)	1.20	1.80	2.30	2.15	2.10	2.25	2.38	1.60	2.50	2.5	2.5	1.25	2.72
pcf width (pcfw)	0.65	1.10	1.17	1.22		1.25	1.20	0.90	1.25	1.2	1.2	0.65	1.67
Heel length (hl)	0.85	1.70	1.70	1.85		1.70	1.80	1.50	1.70	1.8		0.9	1.72
Cal-cuboid width (ccw)	1.25	1.87	2.15	2.02			1.90	1.25	2.35	2.4			2.74
Cal-cub height (cch)	0.90	1.15	1.45	1.35			1.20	1.00	1.50	1.8			2.03
Calcaneal width (cw)	1.80	2.95	3.25	3.25	2.65		2.90	2.16	3.50	3.6	3.7	1.9	3.61
dl/cl	0.52	0.47	0.49	0.47		0.45	0.45		0.49	0.48			0.40
cw/cl	0.42	0.45	0.41	0.43			0.38		0.43	0.44			0.48
hl/cl	0.20	0.26	0.22	0.25		0.22	0.23		0.21	0.22			0.23
pcfl/cl	0.28	0.27	0.29	0.29		0.30	0.31		0.30	0.30			0.36
pcfl/hl	1.41	1.07	1.35	1.16		1.32	1.32	1.07	1.47	1.39		1.39	1.61
pcfw/pcfl	0.54	0.61	0.51	0.57		0.56	0.50	0.56	0.50	0.48	0.48	0.52	0.62
ccw/cch	1.39	1.63	1.48	1.50			1.58	1.25	1.57	1.33			1.34

¹ The extant platyrrhine *Cebuella* is presented for comparison.

the medioplantar region, and the pivot is shifted medially. Morphology-3 calcanei possess relatively flat calcaneocuboid joints resembling those of omomyids and the “unnamed haplorhine group” from Shanghuang. However, the calcaneocuboid joint is round (laterally) in appearance, and part of the medioplantar section has been removed. The pivot has also shifted medially (Fig. 8). Thus, calcaneal morphology 3 is more similar to telanthropoids than it is to omomyids and the “unnamed haplorhine group” from Shanghuang (Gebo et al., 2000b).

Summary. The relatively short distal region, short heel, and calcaneocuboid joint shape distinguish these calcanei from those of any prosimian group known from Shanghuang or elsewhere. These similarities are shared with telanthropoids. Adapiforms also have short distal calcanei, but adapiforms differ from telanthropoids in having a long heel, a long, ribbon-like pcf, and a differently shaped calca-

neocuboid joint. In terms of overall calcaneal proportions and shape, these 12 calcanei are most similar to those of platyrrhines, especially *Saimiri sciureus*, *Saguinus leucopus*, and *Aotus trivirgatus* (Table 2). Functionally, the short, broad calcaneus and relatively long midcalcaneal region imply a mixture of quadrupedalism and leaping (perhaps similar to the locomotor profiles of *Saimiri*; Fleagle and Mittermeier, 1980; Boinski, 1989), with a reduced emphasis on climbing or quadrupedal suspensory movements compared with the unnamed haplorhine calcanei.

Morphology 4. Protoanthropoids: new taxon (fissures A, D, and E; specimens V 12287–12296; Table 6)

Allocation. All examples of morphology 4 come from fissures A, D, and E (Fig. 9). The adapids and *Macrotarsius* from fissure D are too large for these small calcanei, but *Eosimias* fits well in terms of



Fig. 7. Eosimiid calcaneus (left, IVPP V 11851) Top: Lateral and medial views. Bottom: plantar and dorsal views. Scale bar = 2 mm.

size. These calcanei are not at all morphologically similar to *Tarsius*. Thus, on the basis of described dental specimens, *Eosimias* is clearly the best choice for allocation. In terms of morphology, these calcanei are also rather anthropoid-like. However, for reasons outlined above, we believe that morphology 3 is best allocated to Eosimiidae. Thus, we assign these calcanei to a new taxon of early anthropoids from the Shaunguang fissures.

Size. All of the new protoanthropoid calcanei yield body mass estimates less than 125 g. There appear to be 3–5 size classes in this sample. One of the distinguishing features of this group is a wide sustentaculum tali; thus, mass estimates from calcaneal width are larger than those derived from other dimensions, and may inflate the averages.

Morphology. These calcanei are all incomplete distally except for V 12292. V 12288, V 12289, V 12292, V 12294, and V 12295, however, all exhibit parts of the anterior plantar tubercle and thus can-

not be much longer. Morphology 4 calcanei exhibit very moderate distal elongation (40–46%). These values are very similar to those of platyrrhines and to *Cantius mckennai* (Table 2; see especially *Cebus albifrons* and *Saimiri sciureus*). The higher calcaneal width-to-length ratio in these specimens (51%) is thus even more similar to platyrrhines than are eosimiids. All of these calcanei possess a very wide sustentaculum tali, a distinctive feature relative to the other Shaunguang calcanei. Among telanthropoids, propliopithecids also exhibit such a wide sustentaculum (Gebo and Simons, 1987). The heel is about the same proportion of total calcaneal length as in eosimiids and telanthropoids, indicating that it is relatively short compared to that of prosimians.

The pcf/heel ratio is lowest in V 12287 (longest heel); V 12288, V 12290, V 12295, and V 12296 have heels and facets of about equal length, and the other specimens have relatively long facets and short heels. All values are comparable to those in eosimiids. The pcf/wl ratio is similar to that in other haplorhine groups. The anterior calcaneal facet is continuous. The peroneal tubercle is prominent in V 12290, moderate in most specimens, and small in V 12295. Unfortunately, the calcaneocuboid joint is not well-preserved in any specimen. However, the joint is clearly wider than high (Table 6) and wider than most other Shaunguang calcanei.

Summary. Morphology-4 calcanei possess the shortest distal segments, and generally have very platyrrhine-like proportions. Like eosimiids, they retain fairly long posterior calcaneal facets, as do prosimians. The wide sustentaculum tali and very short distal segment of this group distinguishes them from morphology 3 (eosimiids). This calcaneal morphology suggests increased use of quadrupedalism and climbing. Calcaneal features associated with leaping are lacking in this morphological group.

Tali

Haplorhine and strepsirhine tali are easily distinguished on the basis of the shape of the fibular facet and the relationship of the medial talotibial facet and the groove for flexor fibularis (Gebo, 1986a; Beard et al., 1988). Fifteen haplorhine tali were found in fissures A, C, D (most specimens), and E (Fig. 4). Like the calcanei, these haplorhine tali can be divided into four morphological types, two prosimian-like and two anthropoid-like.

The tali are from primates in the same size range as those represented by calcanei, with the exception that the very smallest size class (<30 g) is not represented. In terms of size, only V 12297 and V 12300 are small enough to belong to the small unnamed haplorhine or tarsiid calcanei. Many tali from fissures C and D match the size of eosimiid and new protoanthropoid calcanei. Thus, like the locality information, size alone is not sufficient to match these tali with the appropriate calcaneal morphology. All

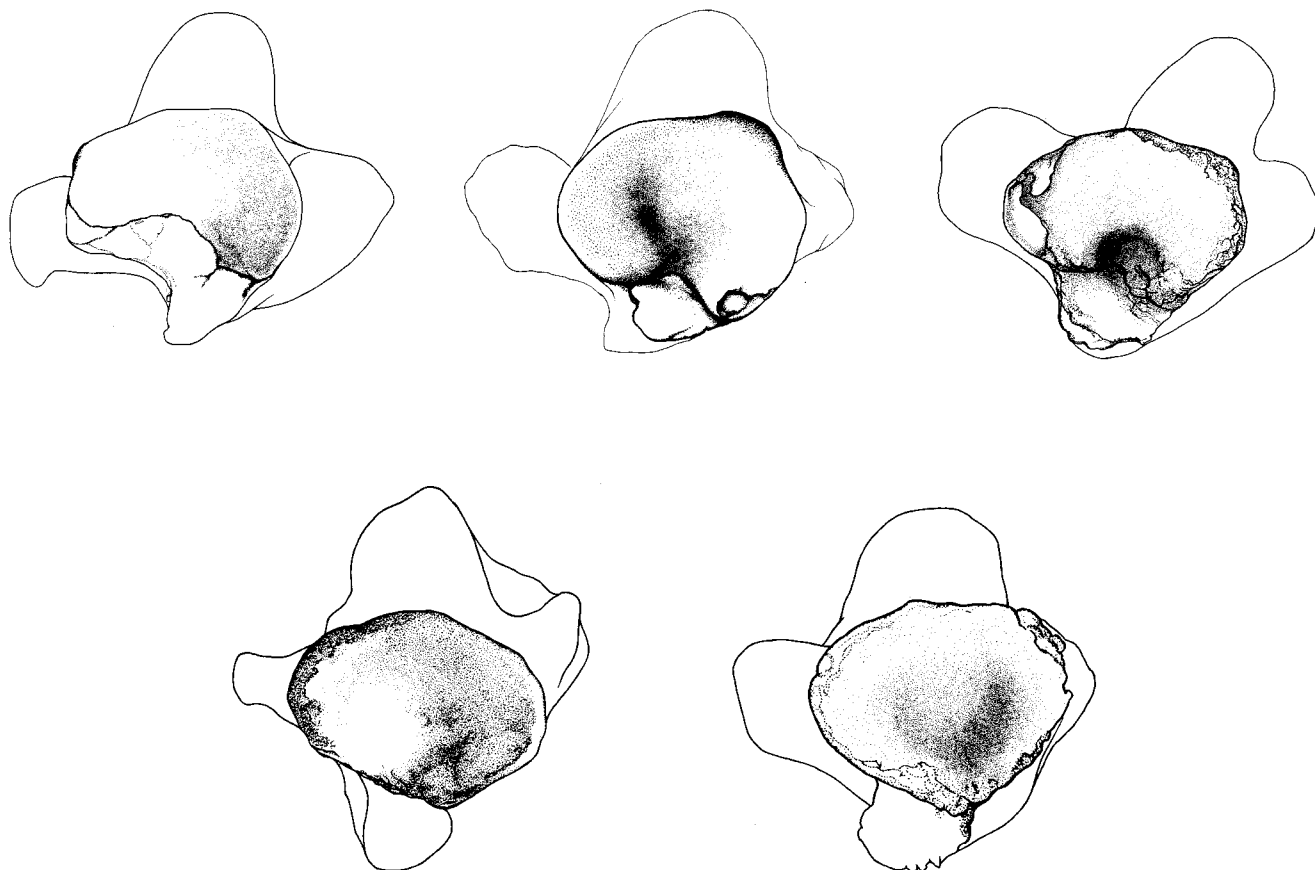


Fig. 8. Haplorhine calcaneocuboid joints (left calcanei; Top, left to right: *Saimiri* (NIU specimen), *Eosimias* (IVPP V 11848), *Eosimias* (IVPP V 11851). Bottom, left to right: *Hemicacodon* (AMNH 126626) and “unnamed haplorhine” from Shanghuang (IVPP V 11853). All specimens are drawn to approximately the same mediolateral width.

of the haplorhine tali are too small for either the Shanghuang adapiforms or the much larger omomyid, *Macrotarsius*. Comparative data for talar indices are given in Table 7.

Morphology 1. Prosimians: unnamed haplorhine family (fissures A and D; specimens V 11857 and V12297–12300; Table 8)

Allocation and size. These tali (Fig. 10) are allocated to the “unnamed haplorhine family” on the basis of their great similarity to omomyid primates. The tali fall into two size classes (Table 1), one of which (V 12297 and V 12300) corresponds to the calcanei V 12275 and V 11853 (30–50 g). The other tali (V 12298–12300) indicate a size class (90 g) of unnamed haplorhines which is currently unrepresented among the calcanei. V 11857 (~60 g) is intermediate. No unnamed haplorhine talus can be matched with the largest unnamed haplorhine calcaneus (V 12276, ~350 g).

Morphology. Talar body morphology is very reminiscent of omomyids. The talus is narrow relative to its length (index tw/tl ; Table 8), as in omomyids and tarsiers; telanthropoids have slightly wider tali. The talar body is tall relative to trochlear width ($lbh/mtrw$) or trochlear length (ht/trl), with a grooved

trochlear surface and parallel trochlear rims. The lateral trochlear rim extends well above the trochlear surface, and the proximal part of this rim extends beyond the body, forming an extension or spike onto the talar neck. This type of trochlear extension is observed in a variety of primates, including some specimens of *Saimiri* and *Apidium*. The medial rim shows little curvature and extends to the edge of the neck. The medial facet is full and prosimian-like. A posterior shelf is present but slight.

The talar neck angle ($16\text{--}24^\circ$) is moderately angled and similar to that in *Tarsius* and omomyids, but less than in platyrrhines. The length of the neck and head is about 50% of total talar length (index nl/tl , Table 8), and slightly greater than the length of the trochlea. These values are similar to those of omomyids; platyrrhines generally have talar necks that are a higher proportion of talar and trochlear length. Tarsiers have relatively short talar necks. Talar head angles range between $28\text{--}36^\circ$. The talar head is elevated on the lateral side and is rotated in this direction as well. These tali differ somewhat from those of omomyids and tarsiers in possessing large talar heads that are broad relative to their height (index hht/hw , Table 8).



Fig. 9. Protoanthropoid calcaneus (right, IVPP V 12288) Top: Lateral and medial views. Bottom: Plantar and dorsal views. Scale bar = 2 mm.

Summary. Talar morphology 1 is phenetically most similar to that of omomyids, and these primates would likely have behaved similarly as well. The low neck angles, long necks, tall bodies, grooved trochleas, and parallel trochlear rims suggest fair leaping capabilities.

Morphology 2. Prosimians: tarsiid (fissure D; specimen V 11854; Table 8)

Allocation and size. This talus (Fig. 4) is distinctive enough to be considered a second talar morphology at fissure D. It shares a few features with extant *Tarsius*, and thus might be best assigned to Tarsiidae. V 11854 is estimated to weigh about 73 g, similar to the largest tarsiid calcanei. No tali have been found which match the smaller size class of tarsiid calcanei.

Morphology. The talar body is higher than in *Tarsius*, but lower than in most other Shanghuang tali. The body is wide relative to other Shanghuang tali ($tw/tl = 58$). Tarsiids also have relatively wide bodies. The trochlear surface is wedged and shallow in

V 11854, with some central grooving. The posterior trochlear shelf is small in V 11854 but larger than that of *Tarsius*, which lacks this feature. V 11854 also possesses a full medial facet, a characteristic of prosimian primates. The medial facet extends onto the talar neck and curves very little medially. The tibial malleolar concavity is shallow.

Compared to morphology-1 tali, V 11854 exhibits a short talar neck ($nl/trl = 87$; $nl/mtrw = 107$) and a low neck angle (22°). These two talar features are reminiscent of *Tarsius*, suggesting a possible allocation to this family. Like the new haplorhine tali, V 11854 possesses a high lateral region of the talar head, but with little dorsolateral head rotation (20°). In extant *Tarsius*, the talar head is dorsomedially oriented, in striking contrast to V 11854. The talar head is ovoid, as is typical of most prosimians, and contrasts with the more triangular head of *Tarsius* (Godinot and Dagosto, 1983; Gebo, 1987a). The distoplantar surface of the talar head, however, does form a slight point in V 11854 rather than the more typical rounded contour. This is similar to *Tarsius*, although certainly not as extreme. The talar head is narrow ($hw/hht = 127$; $hw/mtrw = 89$), another similarity to *Tarsius* and a distinction from the unnamed haplorhines (Table 7).

Summary. V 11854 shares only a few features with the extant genus *Tarsius*, and it certainly lacks most of the highly specialized talar features peculiar to this genus (Gebo, 1987a). However, the V 11854 talus differs from the unnamed haplorhine tali in ways that make it more tarsiid-like. Its short neck and small head, as well as its wide and wedged trochlear surface and lower body height, contrast dramatically with those of the unnamed haplorhine tali (but are reminiscent of tarsiids). Both the unnamed haplorhine tali and V 11854 share low neck angles, full medial facets, shallow tibial concavities, and small trochlear shelves, features characteristically found in a variety of leaping prosimians. The wedged trochlea of V 11854 suggests enhanced dorsoflexed foot positions, implying functionally greater use of vertical supports. If V 11854 does indeed belong to a tarsiid, its distinctive morphology suggests allocation to a genus other than *Tarsius*.

Morphology 3. Protoanthropoids: eosimiids (fissures D and E; specimens V 11849, 11855, V 12301–12304, and V 12312; Table 9)

Allocation and size. The third talar morphology has exemplars at fissures D and E (Fig. 11). The most salient feature of these tali, differentiating them from the previous groups, is their possession of a reduced medial facet for the tibial malleolus. This feature also distinguishes telanthropoid from prosimian primates (Gebo, 1986a). Thus, these tali are best attributed to one of the anthropoid-like groups from Shanghuang. Our attribution to Eosimiidae rather than the “new protoanthropoid” group is based on an additional source of information. Eo-

TABLE 6. Calcaneal measurements (in mm) and ratios for morphology 4

	V 12287	V 12288	V 12289	V 12290	V 12291	V 12292	V 12293	V 12294	V 12295	V 12296
Calcaneal length (cl)	5.1	7.2	5.9			5.8				
Distal length (dl)	2.1	2.9	2.75			2.5		2.65		
pcf length (pcfl)	1.25	2.1	1.85	2.0	2.4	1.8	2.5	2.3	1.7	2.25
pcf width (pcfw)	0.85	1.35	0.95	1.15	1.35	1.10	1.29	1.10	0.90	1.35
Heel length (hl)	1.75	2.2	1.30	1.82	1.90	1.5	2.0		1.85	2.50
Cal-cub width (cew)								1.75	1.75	
Cal-cub height (cch)								1.00	1.10	
Calcaneal width (cw)	2.30	3.5	2.8	3.25	3.44	2.93		2.94	2.90	3.75
dl/cl	0.41	0.40	0.47			0.43				
cw/cl	0.45	0.49	0.47			0.51				
hl/cl	0.34	0.31	0.22			0.26				
pcfl/cl	0.25	0.29	0.31			0.31				
pcfl/hl	0.71	0.95	1.42	1.10	1.26	1.20	1.25		0.92	0.90
pcfw/pcfl	0.68	0.64	0.51	0.58	0.56	0.61	0.52	0.49	0.53	0.60
cew/cch								1.75	1.59	

simiids have also been found at Locality 1 in the Yuanqu Basin of central China (Beard et al., 1996). In contrast to the great diversity of primates at Shanghuang, at Locality 1 in the Yuanqu Basin only two primates are known to occur, *Hoanghoniuss stehlini* and *Eosimias centennicus*. These two taxa are easily distinguished by size, and a primate talus from this locality (V 11846) is clearly in the size range of *Eosimias centennicus*. This specimen is most similar morphologically to the Shanghuang specimens designated as morphology 3. Thus, allocation of these specimens to Eosimiidae is our most secure designation.

There are three size classes of eosimiid tali, matching all but the smallest eosimiid calcanei. With the exception of V 12279, calcanei attributed to the unnamed haplorhines and the tarsiids are too small to be associated with these tali. The “unnamed haplorhine” calcaneus V 12276 is too large to fit well with any of these tali.

Morphology. The moderately tall talar body is similar to that in a variety of primates, with ranges agreeing best with omomyids, cebines, and aotines (ht/mtrw; Table 9). Talar width ratios show these bones to be rather narrow relative to total length, especially relative to platyrrhines and adapiforms, comparing best with *Tarsius* and omomyids (tw/tl; Table 7). The eosimiid tali possess the largest posterior trochlear shelves of all Shanghuang haplorhine tali, being most similar in size to those of omomyids (e.g., *Hemiacodon*). Compared with other primates, the trochlear shelves of eosimiid tali are smaller than those of microchoerids or adapiforms, but larger than those of telanthropoids (including anthropoids from the Fayum and extinct platyrrhines such as *Dolichocebus*). The trochlea is shallow, with fairly parallel trochlear rims. The medial trochlear rim curves medially and extends onto the neck. The posteromedial side of V 11849 and V 12303 possesses a posteromedial facet similar to those of *Aotus* and *Callicebus* (see Gebo et al., 1990). V 12302 and V 11855 possess smaller protuberances in this region.

The angle of the talar neck is moderately high (21–30°), values that are higher than those found among the unnamed haplorhines, omomyids, and tarsiids, but lower than occur in telanthropoids or morphology-4 tali (Table 7). The talar neck is about half of total length (index nl/tl), and equal to trochlear length; the values for these indices are similar to morphology 1 and omomyids, but are lower than usual in telanthropoids.

The talar head angle is 9–20°, similar to all groups of primates. The shape of the talar head is oval to round. The talar head is relatively broad (hw/hht and hw/mtrw) compared to most omomyids and tarsiids; eosimiids are similar to morphology 1 and morphology 4 in this regard.

The medial (or tibial) facet extends onto the medial surface of the talar neck. The medial edge of the talar body extends outward into a protuberance behind the insertion or crease for the posterior talotibial ligament. This region possesses a small (V 12302 and V 11855) to moderate-sized (V 11849) protuberance. This feature occurs among some platyrrhines, cercopithecids, and hominoids, but is rare among omomyids and absent in adapiforms. The eosimiid tali have a prominent posterolateral notch, a feature that is not present among the other Shanghuang tali.

Summary. The tali of eosimiids exhibit one important anthropoid-like feature, the reduction of the medial facet. In other ways, they are unlike anthropoids and resemble omomyids. We interpret these as shared primitive resemblances. Platyrrhines differ from eosimiids in possessing a more grooved trochlear surface, a reduced posterolateral tubercle along the region of the posterior shelf, a very reduced or absent posterior trochlear shelf, and a more laterally rotated talar head. Parapithecids and proploipithecids differ from eosimiids in similar ways. Proploipithecids share a deep medial malleolar concavity with these Shanghuang tali, while parapithecids distinguish themselves from the Shanghuang specimens in possessing a much taller talar body, a reduced posterolateral trochlear tubercle, and plan-

TABLE 7. Talar ratios¹

No.	NL/TL	NL/TRL	NL/MTRW	HT/MTRW	HT/TRL	MTRW/TRL	HW/HHT	HW/MTRW	TW/TL	TNECKANGLE
Omomyids										
1	52	105	122	116 (115-118)	99	86	140	90	57	30
3	55 (54-57)	106 (100-110)	144 (127-165)	144 (127-165)	99	79 (67-79)	140	90	57 (55-60)	30
1	54	103	150	118	70	67	122	100	51	28
3	52 (50-55)	107 (103-112)	142 (134-155)	115 (113-116)	89 (89-90)	76 (72-79)	115 (102-138)	98 (93-105)	51 (50-51)	30
8	51 (49-54)	101 (96-105)	123 (115-135)	107 (98-119)	89 (84-97)	82 (74-91)	124 (118-135)	95 (89-105)	56 (55-61)	25
10	51 (48-57)	99 (93-111)	126 (104-146)	110 (96-118)	86 (77-92)	75 (67-82)	126 (116-124)	94 (78-110)	57 (53-61)	25
1	52	90	135	118	78	66	106	00	52	30
1	58	98	135	126	88	78	112	87	47	26
1	52	72	124	113	70	62	103	89	54	30
Tarsids										
9	49 (40-61)	87 (72-121)	99 (84-118)	76 (67-87)	68 (55-80)	89 (71-104)	118 (114-124)	81 (76-84)	52 (44-56)	17
6	49 (45-54)	89 (76-105)	98 (84-118)	80 (68-96)	73 (60-86)	92 (84-111)	124 (123-125)	87 (82-92)	51 (46-58)	18
Platyrrhines										
1	54	94	125	109	82	75	84	91	65	32
1	60	104	141	108	79	73	84	91	64	35
1	59	90	132	103	76	74	106	109	68	32
1	54	105	136	105	81	77	110	115	59	35
7	63 (55-69)	114 (94-124)	125 (109-135)	87 (81-91)	79 (70-86)	91 (82-95)	121 (112-136)	86 (82-91)	61 (59-64)	42
10	66 (60-72)	125 (112-143)	129 (112-145)	89 (82-95)	86 (82-93)	97 (91-104)	124 (111-136)	88 (83-95)	65 (58-74)	40
6	64 (59-67)	124 (114-132)	134 (129-141)	88 (83-92)	81 (78-85)	92 (87-102)	131 (119-140)	94 (87-101)	61 (59-63)	38
3	59 (59-60)	116 (103-120)	154 (149-157)	108 (103-111)	72 (71-72)	82 (81-85)	120 (118-124)	110 (108-111)	62 (58-65)	37
4	60 (57-63)	111 (105-126)	138 (131-150)	100 (95-108)	74 (67-77)	84 (82-84)	117 (114-120)	101 (98-105)	66 (63-69)	34
20	59 (51-64)	106 (100-122)	121 (102-132)	91 (78-101)	76 (67-84)	88 (80-93)	118 (111-127)	88 (80-95)	65 (60-71)	37
10	60 (54-66)	111 (101-130)	125 (110-141)	85 (81-89)	76 (70-82)	89 (82-94)	125 (119-142)	92 (87-96)	69 (60-75)	38
10	54 (48-61)	99 (87-103)	133 (112-150)	108 (100-117)	76 (69-85)	85 (80-90)	130 (124-137)	98 (91-120)	58 (53-64)	30
6	57 (54-61)	97 (94-105)	118 (114-122)	104 (100-106)	86 (77-91)	82 (77-86)	122 (116-133)	94 (92-98)	66 (61-71)	32
5	56 (53-62)	101 (95-103)	146 (139-159)	134 (127-143)	90 (86-97)	67 (60-71)	127 (118-138)	123 (119-132)	70 (68-73)	33
2	52 (52-53)	91 (89-94)	144	118 (117-119)	82 (80-84)	77 (76-77)	131 (125-136)	118 (115-121)	56 (55-58)	34
3	51 (49-53)	85 (83-87)	125 (110-138)	112 (103-121)	83 (73-94)	77 (68-84)	142 (140-146)	102 (100-104)	59 (58-61)	30
6	53 (53-55)	96 (92-100)	144 (131-153)	119 (112-126)	77 (73-81)	83 (77-86)	131 (125-139)	110 (99-121)	54 (51-56)	31
Adapiforms										
4	46 (41-50)	81 (71-88)	138 (129-148)	120 (112-129)	74 (69-81)	62 (54-67)	129 (125-136)	123 (118-127)	50	15
2	40 (40-41)	77 (65-89)	131 (124-139)	130 (116-141)	82 (82-82)	58 (55-62)	129 (125-136)	123 (118-127)	50	14
4	46 (42-51)	86 (79-91)	146 (126-164)	152 (143-161)	85 (82-88)	55 (48-64)	121 (119-122)	128 (125-132)	59 (58-59)	26
10	43 (40-45)	82 (75-93)	139 (119-161)	158 (138-185)	93 (85-110)	58 (45-66)	123 (122-125)	128 (109-139)	57 (53-63)	35
7	43 (41-46)	72 (67-77)	136 (120-163)	149 (133-167)	78 (69-84)	53 (47-60)	130 (126-133)	130 (120-142)	59 (55-62)	29
2	33 (32-33)	50 (50-51)	80 (78-84)	117 (114-121)	73 (72-75)	62 (59-65)	127	116	67 (63-72)	38
5	37 (31-43)	60 (43-75)	91 (83-101)	124 (100-150)	80 (68-99)	66 (52-79)	132	128	65 (55-82)	37

¹ NL, talar neck length; TL, talar length; TRL, trochlear length; MTRW, midtrochlear width; HT, lateral body height; HW, talar head width; HHT, talar head height; TNECKANGLE, angle of talar neck to talar body; TW, talar width; (), range of values.

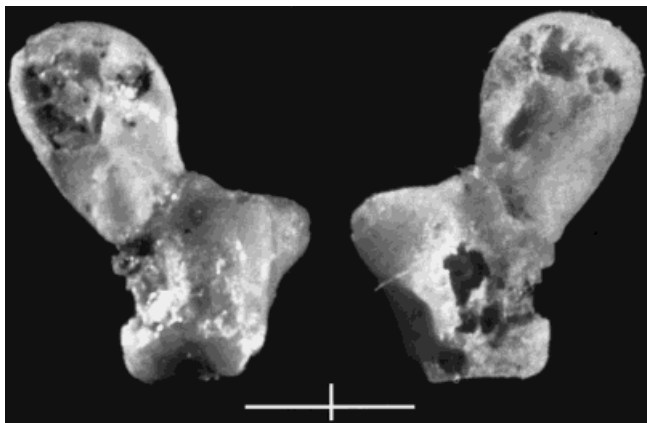


Fig. 10. “Unnamed haplorhine” talus (right, IVPP V 11857). Left to right: Dorsal and plantar views. Scale bar = 2 mm.

tar facets that are morphologically distinct (Gebo and Simons, 1987).

In terms of overall function, the moderate body height and neck angle, the shallow trochlea, and the medial curvature of the trochlear rim imply more moderate leaping abilities for eosimiids than for the unnamed haplorhine or tarsiid tali. These tali suggest a more platyrrhine-like locomotor mode that emphasized quadrupedalism and leaping, with leaping likely being more frequent than among extant platyrrhines (e.g., *Saimiri*). The reduced medial facet suggests a foot adapted for more horizontal branches (Gebo, 1986a).

Morphology 4. Protoanthropoids: new taxon (fissure C; specimens V 12305 and V 12306; Table 9)

Allocation and size. V 12305 and V 12306 represent the fourth talar morphology from Shanghuang (Fig. 12). Both specimens yield size estimates of 65–70 g, which matches the smaller “new protoanthropoid” calcanei, but also overlaps the other groups. However, no “new protoanthropoid” calcanei are yet known from fissure C. The wedge-shaped, flattened trochlea distinguishes these tali from any of the other Shanghuang groups. These features are shared with telanthropoids, particularly platyrrhines, and thus we allocate them to the anthropoid-like group. Based on differences (detailed below) between these tali and the *Eosimias* talus from Locality 1 in Shanxi Province, we allocate these specimens to a separate, unnamed “protoanthropoid” group.

Morphology. The talar body is of moderate height (index ht/mtrw, Table 9) but is very flat on its trochlear surface like omomyids. The anterior edge of the trochlea is wider than the posterior margin, giving a wedge shape that is also found in tarsiers and callitrichids, but is unlike the condition in omomyids. The proportions of the trochlea and talus (mtrw/trl and tw/tl; Tables 7 and 9) are similar to those of eosimiids, omomyids, and *Tarsius*; the talus and

trochlea are relatively longer and narrower than in telanthropoids. A posterior trochlear shelf is present but slight (smaller than in the eosimiids), in contrast to telanthropoids, where it is absent completely. The medial tibial concavity is shallow, but the medial sides of these tali are damaged in both specimens. Therefore, we cannot definitively determine the nature of the medial facet.

Like eosimiids, these tali have long talar necks relative to tarsiids, but shorter necks than in platyrrhines. The talar neck is deflected farther medially (neck angle, 33–35°) than is the case among other Shanghuang primates or Tarsiiformes. Platyrrhines also exhibit generally higher values for the neck angle (Table 7). The talar neck is very pinched at its base.

The talar head is mediolaterally wide and is horizontally positioned (head angle, 15–18°) relative to the body, being rotated laterally. The talar head is oval, and the lateral articular surface is larger than the medial, in contrast to eosimiid tali, in which the two halves are more nearly equal. Talar head ratios (hw/hh; hw/mtrw) show similarities to eosimiid tali as well as to those of aotines and callitrichines (Tables 7 and 9). Omomyids have somewhat narrower talar heads.

Summary. This group differs from the “unnamed haplorhines” and omomyids in its wedge-shaped trochlea, smaller posterior trochlear shelf, and higher angle of the talar neck. In these features, group 4 resembles platyrrhines.

V 12305 and V 12306 differ from eosimiid tali in their higher neck angle, lack of a medial protuberance, and smaller trochlear shelf. The strong pinching at the base of the talar neck also distinguishes this group from eosimiids. Functionally, the wide neck angle, moderate body height, curvature of the medial rim, flattened trochlea, and trochlear wedging suggest far less leaping ability than in the eosimiids. Similarities to cebines and aotines also support an emphasis on quadrupedalism and climbing.

Shanghuang adapiforms: allocation (fissures A and D, specimens V 12307–12309; Table 10)

Calcaneus. A calcaneus (V 12308) found at fissure A may belong to the Adapidae. It is, however, severely damaged, revealing few good anatomical details. The posterior calcaneal facet is preserved and is long, narrow, and well-delineated along its plantar edge, features typical of adapiforms. This calcaneus belonged to a primate far larger than the haplorhine material from Shanghuang, with the sole exception of V 12276. The length of the posterior calcaneal facet length gives a body mass estimate of 421 g. Another potential adapid calcaneus at fissure D (V 12309) yields a body mass estimate of 390–475 g. Beard et al. (1994) noted two adapiform taxa from fissures B and D, *Adapoides troglodytes* (fissures B and D, *Microadapis*-sized, ~200 g) and a larger unnamed *Europolemur*-like form (fissure D). These cal-

TABLE 8. Measurements (in mm) and ratios for prosimian tali

	Unnamed haplorhines					Tarsiid V 11854
	V 11857	V 12297	V 12298	V 12299	V 12300	
Talar length (tl)	4.9		6.10	5.92		4.75
Talar width (tw)	2.49	2.1	2.92	2.66		2.76
Trochlear length (trl)	2.53	1.9	2.53	2.60		2.60
Midtrochlear width (mtrw)		1.6	2.12	2.00	1.59	2.13
Head height (hht)	1.58		1.51	1.60		1.49
Head width (hw)	2.13		2.25	2.20		1.89
Neck length (nl)	2.64		3.17	3.03		2.25
Lateral body height (lbh)	1.91	1.9	2.36	1.98	1.36	2.06
Lateral body length (lbl)	2.57	2.1	2.58			2.53
Postfacet length (pcfl)		1.5	2.1			1.75
Postfacet maximum width (pcfxw)	1.2	0.8	1.5			1.3
Postfacet minimum width (pcfnw)		0.7	1.0			0.75
Talar neck angle (degrees)	24	18	16	18		22
Talar head angle (degrees)	28		35	36		20
tw/tl	0.51		0.49	0.45		0.58
lbh/mtrw		1.19	1.11	0.99	0.86	0.97
lbh/trl	0.75	1.0	0.93	0.76		0.79
nl/tl	0.54		0.52	0.51		0.47
nl/trl	1.04		1.25	1.17		0.87
nl/mtrw			1.49	1.52		1.07
hw/hht	1.35		1.49	1.38		1.27
hw/mtrw			1.07	1.10		0.89
mtrw/trl		0.84	0.84	0.77		0.82

canei are smaller than we would expect for the omomyid *Macrotarsius* (900–1,221 g; MacPhee et al., 1995), which is also found at fissure D.

The width-to-length ratio of the posterior calcaneal facet of V 12308 equals 0.39, a low value more similar to those of adapiforms than those of haplorhines. V 12309 also has a low pcf w/l index ratio of 0.40. Pcf w/l ratios for both of these calcanei are lower than those of adapines (Tables 2 and 10). The heel is long, a feature similar to that of *Adapis* and *Leptadapis*.

Talus. A heavily damaged adapid talus (V 12307) was found at fissure A (Fig. 13). From talar width and midtrochlear width, we estimate body mass at 211 g. This is larger than all but one (V 12276) of the haplorhine tarsal elements. Given the size differences between the two calcaneal specimens and the talus (see below), it seems likely that tarsals of two differently sized adapids have been identified among the Shanghuang fissures. The size and morphology (below) of this specimen suggest that the best allocation for this specimen is with the smaller Shanghuang adapiform, *Adapoides troglodytes*.

V 12307 is broken at the proximal edge of the talar head. The plantar surface of the talar body is also severely damaged. One important area that is preserved is the talofibular facet. This facet slopes away from the trochlea, as in strepsirhine primates (Gebo, 1986a Beard et al., 1988; Dagosto, 1988). This feature, as well as the specimen's size, strongly support an adapiform allocation for this talus. The strong medial curvature of the trochlear rim, short talar neck, and high angle of the talar neck (40°) are key morphological similarities to tali allocated to *Adapis* and *Leptadapis* from Europe (Dagosto, 1983; Gebo, 1988; Godinot, 1991). The teeth of *Adapoides* also exhibit similarities to adapines (Beard et al., 1994).

Early Eocene *Cantius* has a low neck angle (11–14°), while later *Cantius*, *Notharctus*, and *Smilodectes* have higher neck angles (15–42°) (Gebo et al., 1991). V 12307 is therefore more similar to later rather than earlier notharctines. The trochlea is very shallow, and the medial facet or tibial malleolar concavity is very deep. The medial facet appears to be full or at least not reduced, but breakage hampers a better assessment. The body is very short relative to the haplorhine tali from Shanghuang (ht/mtrw = 87; ht/trl = 63; Tables 7 and 10). A trochlear shape (mtrw/trl) of 73 and talar shape (width/estimated length) of 75 overlap the upper range of other adapiforms, and are most closely matched by adapines.

From what is known of this talus, it does not appear to be very similar to notharctines. Its low body height, deep tibial malleolar concavity, strong medial curvature of the trochlear rim, short neck, large neck angle, and possible absence of a trochlear shelf are all features that this talus shares with those of *Adapis* (Dagosto, 1983). Like that of *Adapis*, this talar morphology suggests a more quadrupedal climbing-oriented primate with minimal, if any, leaping.

DISCUSSION

Diversity and size

The Shanghuang tarsals represent approximately 12–16 species-level haplorhine taxa plus two adapiforms. The only taxon known from dental remains which is not represented by tarsal elements is the large omomyid, *Macrotarsius*. The tarsal evidence suggests that several as yet unnamed species of haplorhines exist at Shanghuang. The most amazing aspect of this fauna is its diversity of extremely diminutive primates (Gebo et al., 2000a). Only two of the haplorhine taxa represented by tarsal re-



Fig. 11. Eosimiid talus (right, IVPP V 11849). Top, left: Dorsal view. Top, right: Plantar view. Middle, left: Lateral view. Middle, right: Medial view. Bottom, left: Distal view. Bottom, right: Proximal view. Scale bar = 2 mm.

mains appear to exceed 100 g. Twenty-eight percent of the haplorhine specimens yield body mass estimates below 50 g, 51% fall between 50–100 g, and 21% are above 100 g. The smallest primates ever documented (10–15 g) are present in this fauna (Gebo et al., 2000a). *Microcebus myoxinus*-sized primates (30 g) are not uncommon; each of the four haplorhine groups possesses one species in this tiny

size range. Though larger than the haplorhines, the adapiforms are also small, in the 200–500-g size range.

Despite a large overlap in size, the more “prosimian-like” haplorhine taxa are generally smaller than the protoanthropoid taxa. Specimens in the unnamed haplorhine group and the tarsiids fall below 100 g, with one exception: an “unnamed haplorhine”

TABLE 9. Measurements and indices for protoanthropoid tali¹

	Eosimiids							Protoanthropoids		
	V 11847 ²	V 11849	V 11855	V 12301	V 12302	V 12303	V 12304	V 12312	V 12305	V 12306
Talar length (tl)	6.35	5.95	6.20			5.70			5.08	4.95
Talar width (tw)	3.30	2.87	3.34	2.77	2.68	2.95	2.6	2.9	2.85	2.65
Trochlear length (trl)	3.25	3.03	3.25	3.00		3.00	2.5	2.5	2.44	2.59
Midtrochlear width (mtrw)	2.50	2.30	2.30	1.81	2.3	2.25	1.9	2.0	1.75	2.04
Head height (hht)	1.95	1.78	1.79		1.77	1.35 ²			1.41	1.44
Head width (hw)	2.65	2.38	2.39		2.33	2.15	1.85		1.95	1.95
Neck length (nl)	3.25	3.05	3.0		2.86	2.75			2.5	2.45
Lateral body height (lbh)	2.80	2.20	2.9	2.34	2.39	2.65		2.25	2.05	2.10
Lateral body length	3.85	3.42	3.75	2.75		3.15		2.85	2.6	3.00
Postfacet length	2.60	2.3	2.5	2.4		2.50		2.4		2.1
Postfacet maximum width	1.75	1.85	1.9	1.5	1.6	1.75		1.85		1.25
Postfacet minimum width	1.0	1.0	1.1	1.0	1.1	0.90		0.8	0.75	0.8
Talar neck angle	27.0	30.0	29.0	27.0	24.0	30.0	21.0	28.0	35.0	33.0
Talar head angle	15.0	10.0	13.0		9.0	12.0	20.0		18.0	15.0
tw/tl	0.52	0.48	0.54			0.52			0.56	0.54
lbh/mtrw	1.12	0.96	1.26	1.29	1.04	1.18		1.13	1.17	1.03
lbh/trl	0.86	0.73	0.89	0.78		0.88		0.90	0.84	0.81
nl/tl	0.51	0.51	0.48			0.48			0.49	0.49
nl/trl	1.30	1.33	1.30		1.24	1.22			1.42	1.20
nl/mtrw	1.00	1.01	0.92			0.92			1.02	0.95
hw/hht	1.36	1.34	1.34		1.32	1.59 ²			1.38	1.35
hw/mtrw	1.06	1.03	1.04		1.01	0.96	0.97		1.11	0.96
mtrw/trl	0.77	0.76	0.71	0.6		0.75	0.76	0.80	0.72	0.79

¹ Linear measurements in mm; angles in degrees.

² Locality 1 specimen from Shanxi Province, China.

calcaneus from fissure A suggests a primate that weighs about 350 g. Body mass estimates from eosimiid and other protoanthropoid tarsals range from 50–125 g, with two exceptions. An eosimiid calcaneus from fissure D yields a body mass estimate of only 17 g, and a new protoanthropoid calcaneus from fissure A yields a mass estimate of 30 g.

Each fissure displays a characteristic array of tarsal morphs and sizes. Eosimiids and new protoanthropoids are found in all four fissures, the unnamed haplorhines are found in three, and tarsiids are known only from fissure D. Fissure A has the unnamed haplorhines, including a “giant” species (350 g), a small protoanthropoid (30 g), and eosimiids ranging from 80–100 g. Eosimiids are more common at fissure A than are other protoanthropoid specimens, in contrast to the other fissures where these two groups are more evenly abundant. Fissures C and E are similar: both contain eosimiids and the other protoanthropoid group in the 50–60-g size range. Fissure E also has an unnamed haplorhine (30 g), and large (above 100 g) specimens of eosimiids and other protoanthropoids. Fissure D produces the largest number of specimens, and each morphological group is represented. It may contain as many as nine taxa of haplorhines and one adapiform. Only at fissure D do tarsiids and the unnamed haplorhine tarsals co-occur. This diversity of small primates suggests a fine division of the small-branch niche. As discussed above, tarsal anatomy supports the existence of several different locomotor patterns, ranging from a tarsier-like pattern to cheirogaleid-like quadrupedal/leaping.

Phylogenetic relationships

The 11 tarsal characters considered in this paper (the characters and the data matrix are in Tables 11 and 12) were subjected to phylogenetic analysis, using PAUP 4.0 (Swofford, 1998). If all taxa are included, the 50% majority-rule consensus tree (Fig. 14) shows support for grouping the protoanthropoid group and *Eosimias* with telanthropoids; the Shanghuang tarsiids with *Tarsius*; monophyly of Haplorhini (omomyids + *Tarsius* + anthropoids); and monophyly of Adapiformes. Due to the small number of synapomorphies defining any node, the bootstrap values for many of these groupings are quite low. If the protoanthropoid taxon, for which some critical characters are unknown (i.e., the nature of the tibiotalar facet and the nature of the calcaneocuboid joint), is removed from the analysis, both consensus tree and bootstrap support for grouping *Eosimias* with telanthropoids is increased (Gebo et al., 2000b). Other relationships remain more or less unchanged.

Adapiformes. The two adapiforms at Shanghuang are larger (200–400 g) than the small haplorhines, overlapping in size with only the largest haplorhine calcaneus (V 12276). These tarsals are heavily damaged, and besides noting adapine-like similarities suggesting increased climbing and decreased leaping abilities, we cannot say more about their relevance to the Asian and European adapine radiations. The incompleteness of these bones pre-

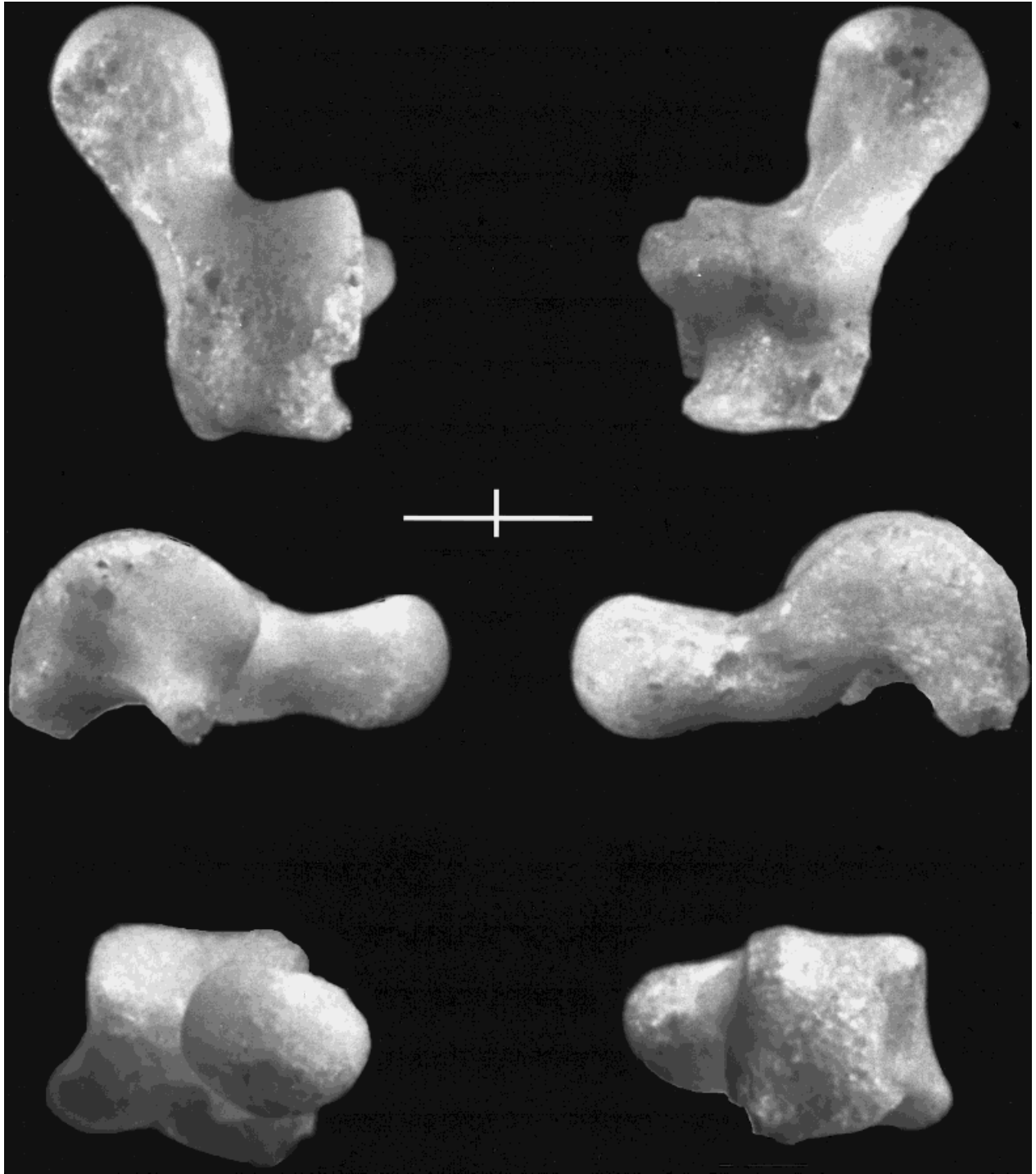


Fig. 12. Protoanthropoid talus (right, IVPP V 12306). Top, left: Dorsal view. Top, right: Plantar view. Middle, left: Lateral view. Middle, right: Medial view. Bottom, left: Distal view. Bottom, right: Proximal view. Scale bar = 2 mm.

cludes their incorporation into the phylogenetic analysis.

Tarsiids. The Middle Eocene tarsals we have attributed to tarsiids indicate one taxon as small as and one smaller than the smallest extant tarsier, *T. pumilus* (about 70–90 g). These tarsals are from postcranially primitive tarsiids, exhibiting only a few of the derived features typical of extant *Tarsius*.

This may imply a less derived locomotor behavior in Shanghuang tarsiids. The phylogenetic analysis links these Shanghuang tarsiids to modern tarsiers on the basis of lower talar body height.

Unnamed haplorhines, morphology 1. The great similarity of the Shanghuang “unnamed haplorhine” tarsals to those of North American omomyids, despite the absence of taxa (other than *Macro-*

TABLE 10. *Adapid tarsal measurements and ratios*¹

	V 12308	V 12309	V 12307
Calcaneal length (cl)			Talar length
Distal length (dl)			5.6 mm ²
pcf length (pcfl)	3.85	3.75	Talar width
pcf width (pcfw)	1.5	1.5	4.2
Heel length (hl)	4.0		Trochlear width
Cal-cub width (ccw)			3.7
Cal-cub height (cch)			Midtrochlear width
Calcaneal width (cw)		5.25	3.0
			Head height
			Head width
			Neck length
			Lateral body height
			2.6
			Trochlear length
			4.1
			Talar head angle
			14°
			Talar neck angle
			40°
dl/cl			Body height/midtrochlear
cw/cl			0.87
hl/cl			Body height/trochlear length
pcfl/cl			0.63
pcfl/hl	0.96		Midtrochlear width/trochlear
pcfw/pcfl	0.39	0.40	0.73
ccw/cch			Talar width/talar length
			0.75 ²

¹ Linear measurements in mm; angles in degrees. pcf, posterior calcaneal facet.

² Estimated value.



Fig. 13. Dorsal view of a left adapiform talus from Shanghuang, China (left, IVPP V 12307), compared to *Adapis parisiensis* (right, unnumbered, Montauban). Scale = 2 mm.

tarsius) that closely resemble North American omomyids in dental morphology, suggests that this tarsal morphology is primitive for haplorhines and perhaps for primates as well. Tali of this group are virtually indistinguishable from North American omomyids, a group that possesses less derived tali than do microchoerids. The unnamed haplorhine calcanei are longer distally than those of North American omomyids (with the exception of V 11847). This group is also unusual in its range of body size. The smallest haplorhine at Shanghuang (about 12 g) belongs to this group, as does the largest (350 g). Given that this unnamed haplorhine group is so similar to North American omomyids in terms of tarsal morphology, other anatomical regions will be needed to sort out their phylogenetic relationships. However, it is clear that this group lacks special similarities to either extant tarsiers or telanthropoids, although it could be a primitive stem for either of these groups. Its most likely phylogenetic position is either a stem haplorhine or a sister taxon to the Omomyidae. In our phylogenetic analysis this group forms an unresolved polytomy with omomyids, tarsiiids, and anthropoids.

TABLE 11. *Characters used in phylogenetic analysis*

1. Shape of talotibial facet	0, steep-sided
	1, steep-sided with a plantar lip
	2, sloped
2. Flexor fibularis groove	0, central to trochlea
	1, lateral to trochlea
3. Talar neck angle	0, <20°
	1, 20–30°
	2, >30°
4. Talar body height (lbh/mtrw*100)	0, <100
	1, 100–120
	2, 120–150
5. Posterior trochlear shelf	0, none
	1, small
	2, large
6. Talar width/talar length (tw/tl*100)	0, <60
	1, >60
7. Medial talotibial facet	0, short (does not reach to plantar edge of bone)
	1, long
8. Relative width of posterior calcaneal facet pcfw/pcfl	0, >50
	1, <50
9. Relative length of distal calcaneus (dl/cl*100)	0, <45
	1, >45
10. Relative length of calcaneal heel (hl/cl*100)	0, long, >30
	1, moderate, 25–30
	2, short, <20
11. Morphology of calcaneocuboid joint	0, fan-shaped, no nonarticular surface
	1, more circular, nonarticular surface present

Eosimiids, protoanthropoids, and anthropoid origins

Our phylogenetic analysis provides support for linking telanthropoids to *Eosimias* and/or the other protoanthropoid group from Shanghuang, to the exclusion of any other primate group considered. Although bootstrap support is low, given the small number of potential synapomorphies (n = 2), boot-

TABLE 12. Data matrix used in phylogenetic analysis

Taxon	1	2	3	4	5	6	7	8	9	10	11
Outgroup	0	1	1	0	0	0	0	0	0	0	0
<i>Eosimias</i>	1	0	1	1	1	0	0	0	1	1	1
<i>Tarsius</i>	1	0	0	0	0	0	1	0	1	2	0
<i>Apidium</i>	1	0	2	1	0	1	0	0	0	1	1
<i>Saimiri</i>	1	0	2	1	0	1	0	0	1	1	1
Anaptomorphinae	1	0	1	1	1	0	1	0	1	1	0
Omomyinae	1	0	1	1	1	0	1	0	1	1	0
Notharctinae	2	1	1	2	2	0	1	1	0	0	0
Adapinae	2	1	2	1	2	1	1	1	0	0	0
Protoadapinae	2	1	?	?	2	?	1	?	0	0	0
Shanghuang "unnamed haplorhines"	1	0	1	1	1	0	1	0	1	1	0
Shanghuang tarsiids	1	0	1	0	1	0	1	0	?	?	?
Shanghuang protoanthropoid	1	0	2	1	1	0	?	0	0	1	?

strap support for linking any other taxon to telanthropoids is even lower, and no such grouping appears among the most parsimonious trees. *Eosimiid* and unnamed protoanthropoid tarsals show a remarkable blend of omomyid (or primitive haplorhine) and telanthropoid characteristics. These two taxa are the first morphologically transitional forms to inform the debate on anthropoid origins. The one characteristic that so far consistently distinguishes the talus of telanthropoids from that of any prosimian primate is the reduced medial talar facet. All of the eosimiid tali exhibit this feature. Yet these same tali also retain features that are otherwise characteristic of omomyid primates. These features include the presence of a posterior trochlear shelf, a relatively narrow talar body, and a low talar neck angle. In some respects, the unnamed protoanthropoid tali are even more platyrrhine-like in their morphology. For example, the wedge-shaped, flattened trochlea found in these specimens is a very platyrrhine-like feature. The wide sustentaculum tali of the unnamed protoanthropoid group is also reminiscent of extant and extinct telanthropoids, including the Propiopihecidae. The most significant features of the protoanthropoid calcanei are the shorter lengths of their distal segments and their overall proportions. In these respects, the unnamed protoanthropoid calcanei are like a variety of small platyrrhines (Table 2). In terms of distal elongation, eosimiid calcanei are slightly longer, but still not significantly different from *Saimiri*. Both groups have much shorter distal calcaneal segments than any known omomyids, tarsiers, or the unnamed haplorhine group. The morphology of the calcaneocuboid joint in *Eosimias* (this region is not preserved in the unnamed protoanthropoid calcanei) provides particularly strong evidence linking this group to telanthropoids.

The protoanthropoid and eosimiid tarsals from Shanghuang display morphology intermediate between that of the Omomyidae and telanthropoids. In conjunction with the dental evidence (Beard et al., 1994, 1996), we take this to mean that the evolutionary transformation from more primitive haplorhines to telanthropoids is documented in part here

among the Shanghuang primates. No other primate tarsals from any other time or place show such a mixture of characteristics as do these particular specimens. It is no surprise to us that omomyid-like features would be found in protoanthropoids, since we argued previously that omomyids and platyrrhines are not so vastly different in tarsal morphology (Gebo and Simons, 1987; Dagosto, 1990; Dagosto and Gebo, 1994). In contrast, the tarsals of adapiforms (including those of early *Cantius*, *Anchomomys*, *Europolemur*, and *Donrussellia*; Godinot, personal communication; D.L.G. and M.D., personal observations) are quite easily distinguished from those of telanthropoids (Beard et al., 1988). Given their intermediate morphology, the oldest known anthropoid postcranial fossils bolster hypotheses favoring the haplorhine affinities of anthropoids and are inconsistent with hypotheses advocating an adapiform origin for higher primates (e.g., Gingerich and Schoeninger, 1977; Rasmussen, 1994; Simons, 1995). Our phylogenetic analysis supports this interpretation as well; adapiforms always form a well-supported monophyletic group, and in none of the most parsimonious trees do adapiform primates form a sister group with anthropoids. The bootstrap support for an adapiform-anthropoid link is <5%.

The importance of *Eosimias* tarsals lies in their unique combination of prosimian-like and anthropoid-like traits. This mosaic of primitive and derived characters in *Eosimias*, a basal member of the anthropoid clade, has substantial implications for understanding anthropoid origins. For example, the combination of primitive and derived tarsal characters in *Eosimias* conflicts with the hypothesis that anthropoid postcranial features are primitive for primates and supports the long-held view that the postcranium of modern anthropoids must be derived from more prosimian-like progenitors. This argues against the recently proposed hypothesis that anthropoids were the first major clade to differentiate from stem primates in the early Cenozoic (Ford, 1986, 1988), which is supported mainly by analyses of postcranial characters (Ford, 1986, 1988; Dagosto and Gebo, 1994). If this hypothesis of character polarity were true, the telanthropoid features among

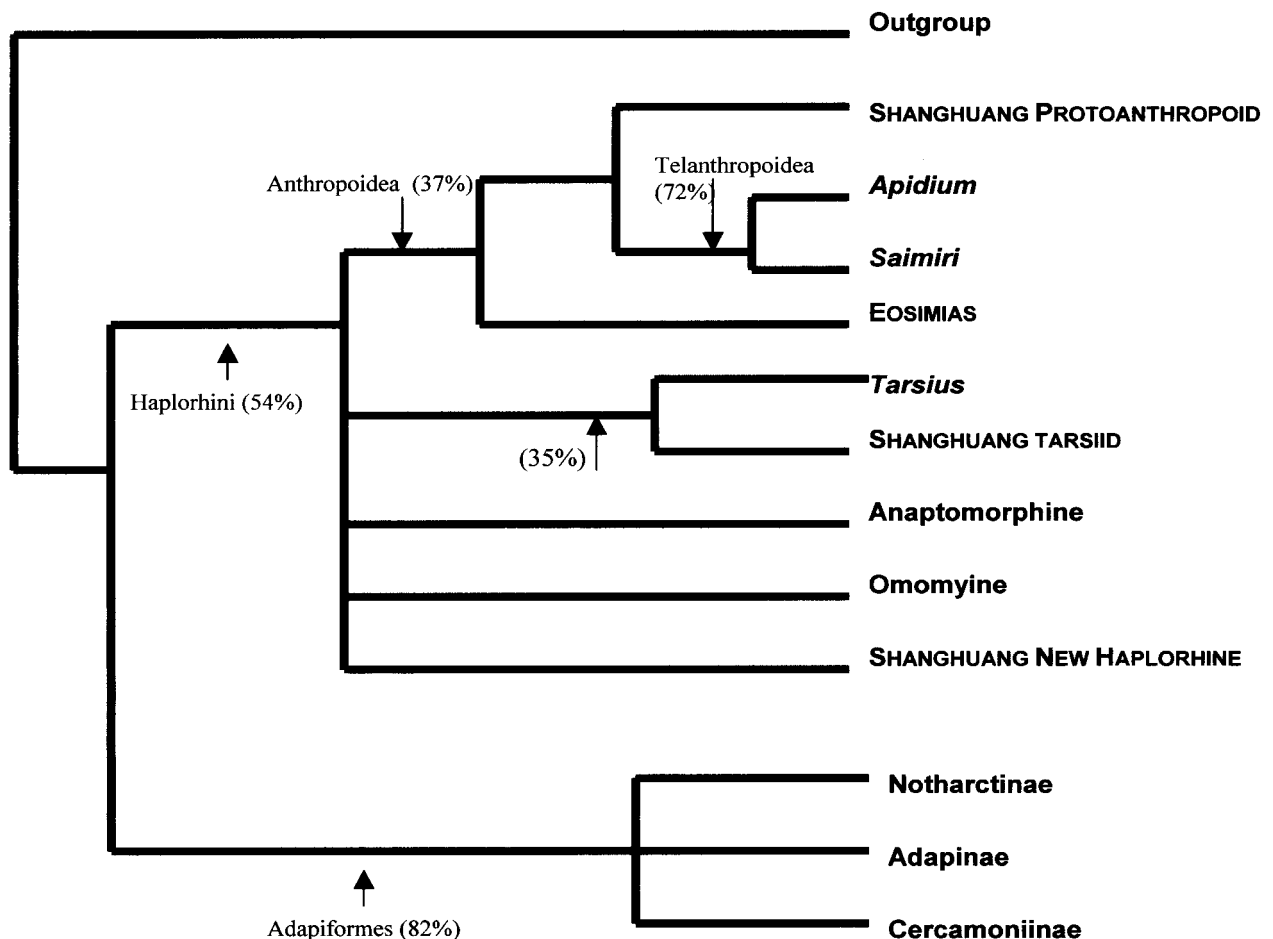


Fig. 14. Parsimony analysis of 11 tarsal characters using PAUP 4.0*. The 50% majority rule consensus tree is shown. The analysis yields the 24 most parsimonious trees with a consistency index of 0.667, a retention index of 0.742, a homoplasy index of 0.333, and a rescaled consistency index of 0.495. Characters are unweighted. Characters with more than two states (1, 3, 4, 5, and 10) are ordered. The analysis is run under ACCTRAN, and is rooted at the outgroup. No other constraints are employed. The “outgroup” consists of character states present in the most likely sister groups of Primates: Scandentia, Dermoptera, and Plesiadapiformes; these taxa differ insignificantly in the expression of these tarsal traits. In all but three trees, *Eosimias* groups with telanthropoids (*Apidium* and *Saimiri*). All trees recognize a monophyletic Haplorhini. Nodes for telanthropoids, Anthropoidea, Haplorhini, and Adapiformes are labeled; the numbers following are the bootstrap values based on 100 replications. The synapomorphies for Anthropoidea are shape of the calcaneocuboid joint and reduced medial talar facet. The synapomorphies for telanthropoids are increased talar neck angle, increased talar width, and loss of posterior trochlear shelf. The synapomorphies for Haplorhini are increased distal length of calcaneus, relatively short heel, a steep-sided talofibular facet with a plantar lip, and a centrally located flexor fibularis groove. The synapomorphies for Adapiformes are a sloping talofibular facet, increased size of the posterior trochlear shelf, a long and narrow posterior talocalcaneal facet, increased size of talotibial facet (medial facet), and increased height of the talar body. The major phylogenetic conclusions of the analysis are unaffected if other platyrrhines (*Aotus*, *Cebus*, *Callicebus*, and *Dolichocebus*) are substituted for *Saimiri* or are included in the analysis. Similarly, early catarrhines like *Aegyptopithecus* have the same character states as *Apidium*, and therefore do not change the results.

the Shanghuang tarsals would have to be explained as documenting a transition from primitive primates to prosimians, a proposition difficult to reconcile with the dental evidence of *Eosimias* and the presence of omomyids and adapiforms in deposits much older than the Shanghuang fauna. *Eosimias* thus helps to document the polarity of the seemingly primitive mammalian character states present in anthropoid tarsals (e.g., the short medial tibiotalar facet), indicating that they are actually anthropoid apomorphies (i.e., reversals from the primitive primate condition), and not retentions from a mammalian ancestor. The optimization of this character in the PAUP analysis most often (63% of most parsim-

onious trees) interprets this character as a derived feature of anthropoids. In a minority of trees, a short facet is interpreted as a primitive retention of haplorhines, independently lengthened in omomyids, tarsiers, and adapiforms. The morphology of the calcaneocuboid joint, however, is unambiguously interpreted as an anthropoid synapomorphy.

If anthropoids were not the first major primate clade to differentiate, they must be more closely related to certain “prosimian” taxa than to others. Resolution of this phylogenetic issue remains controversial, largely because different workers have interpreted the available craniodental evidence in very different ways. As noted above, locating the

origin of anthropoids among adapiform primates is highly unlikely. Precisely how early anthropoids relate to other living and fossil haplorhines continues to be debated, with the three most plausible hypotheses being: 1) anthropoids evolved from Eocene omomyids (Rosenberger and Szalay, 1980); 2) anthropoids share more recent common ancestry with living and fossil tarsiers than they do with any other primates (Cartmill and Kay, 1978; Cartmill, 1980; Ross, 1994; Kay et al., 1997; Ross et al., 1998); and 3) anthropoids diverged early in the Cenozoic from other haplorhines, and their likely sister group consists of a clade including both tarsiers and omomyids (Beard et al., 1991, 1994, 1996; Beard and MacPhee, 1994). The tarsals of *Eosimias* do not provide support for an exclusive tarsier-anthropoid clade. However, it is not possible to distinguish any of these hypotheses from the perspective of postcranial data alone, because omomyid tarsal morphology is very likely primitive for all haplorhine primates, and would have characterized any pretarsioid haplorhine as well. From a consideration of tarsal morphology alone, it is as yet impossible to resolve a trichotomy among anthropoids, tarsiids, and omomyids.

There are, of course, alternative interpretations of this evidence, but they are all less parsimonious. Telanthropoid-like features could have evolved in parallel in a new Asian group of haplorhines, or they could have evolved in parallel among omomyids or tarsiids having no phylogenetic connection to Anthropoidea. The available evidence does not support such claims. In fact, our demonstration that eosimids are morphologically intermediate between later anthropoids and more basal haplorhines (such as omomyids) in both dental and postcranial features considerably strengthens support for the anthropoid affinities of this taxon. Similarly, those who prefer to interpret the Chinese basal anthropoids as some variety of omomyids or tarsiids must now explain the absence of any shared-derived postcranial characters linking these groups, the lack of any strong phenetic resemblance between the tarsals of Shanghuang anthropoids and tarsiids, and the presence of strong phenetic resemblances between omomyids, tarsiids, and other Shanghuang primates (i.e., morphologies 1 and 2).

The protoanthropoid tarsals from Shanghuang are obviously not identical to those of extant telanthropoids (as are the known fossil anthropoid tarsals from Egypt or South America, for example). If they were, the fossils would tell us little about the origin of anthropoids except to note that "true" anthropoids lived in the Eocene of China. We believe that the transitional morphology documented here is much more informative for understanding the timing and pattern of anthropoid origins. The most parsimonious hypothesis is that the Shanghuang specimens pertain to primitive forms that represent the sister group of the large clade that subsumes all extant anthropoids and closely allied fossils from North

Africa, Oman, and South America. Simply put, the Shanghuang anthropoid tarsals bridge the morphological gap between prosimian-grade haplorhines and Anthropoidea, and thereby help to illuminate this poorly documented evolutionary transition.

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